Atlantic Ocean
Colon
Cristobal
Gatun Locks
Rise 85 ft.
Gatun Lake

Missouri Botanical Garden,
an-made fresh water lake,
of watershed silts up. Gatun L

A Letter From Panama:

Dr. William G. D'Arcy

El Barú at an elevation of more than 6,000 feet is serving as a base for my Earthwatch expedition in Panama. This mountain is the highest in Panama and as such is rather cool; it is only 60° here in contrast to the usual 80° at lower elevations.

Our expedition is made up of an interested and dedicated group of people. I should tell you that Earthwatch is an organization that serves as a clearinghouse matching people's interests with projects that need interested people. Projects include research in almost all areas of endeavor.

I'm pleased to be participating in this particular project because it makes it possible to survey the vegetation and document a recently established national park. This data will provide the basis for land use planning.

We made more than 2,000 collections in the two expeditions — several specimens discovered and several rediscovered. Others that were known in other Central American countries were found here as well.

This trip allowed me to make further preparation for our symposium in April, 1980. I met with the local committee and we have been making preparations for translators, meeting places and hotels in Panama City. Attendance will number 400 or more from all over the world. The papers presented will cover all of the natural history aspects of Central America. Conservation will be the key issue.

As a result of this symposium, a color pictorial volume will be published containing all papers presented. The book will provide a resource volume for anyone interested in the natural history of Central America and Panama. There are 60 invited speakers whose papers will be included.

I've made progress in making arrangements for the exciting event. I'll return next October, but all goes well so far.

— Bill D'Arcy

Dr. William G. D'Arcy is an Associate Curator and is editor of the Flora of Panama.

A Festschrift for William G. D'Arcy

The Legacy of a Taxonomist

Edited by
Richard C. Keating
Victoria C. Hollowell
and Thomas B. Croat

Missouri Botanical Garden Press

The life of William G. D'Arcy was unusual in many respects. His research career as a systematic botanist would be considered exceptionally productive even if begun in his twenties, rather than at age 41 when most scientists are already in mid-career. A native of western Canada, D'Arcy developed early natural history interests. In college he concentrated on economics, not visualizing making a living in natural history. In his early career he worked as an economist, and then as an entrepreneur in the British West Indies. In that beautiful locale, a fascination with the local flora gradually attracted more and more of his energy. Deciding on a career change, D'Arcy pursued master's (University of Florida) and doctoral (Washington University) degrees. In each case his thesis treated the nightshade family, Solanaceae, the plant family that remained his life-long passion.

During his doctoral work, D'Arcy was exposed to the Missouri Botanical Garden's program in Panamanian floristics. With this field experience and Ph.D. in hand, he was appointed by the Garden to organize the completion of the multi-volume *Flora of Panama* project. Coordinating a network of collaborators, he accomplished this to a high standard within a decade. Simultaneously, he developed the first computerized database for a large flora. Over the years at Missouri he rose to the rank of Curator and became an internationally recognized expert in the systematics and evolution of the large and economically important nightshade family. By himself, and with numerous collaborators and students, D'Arcy investigated many structural and physiological phenomena impinging on the

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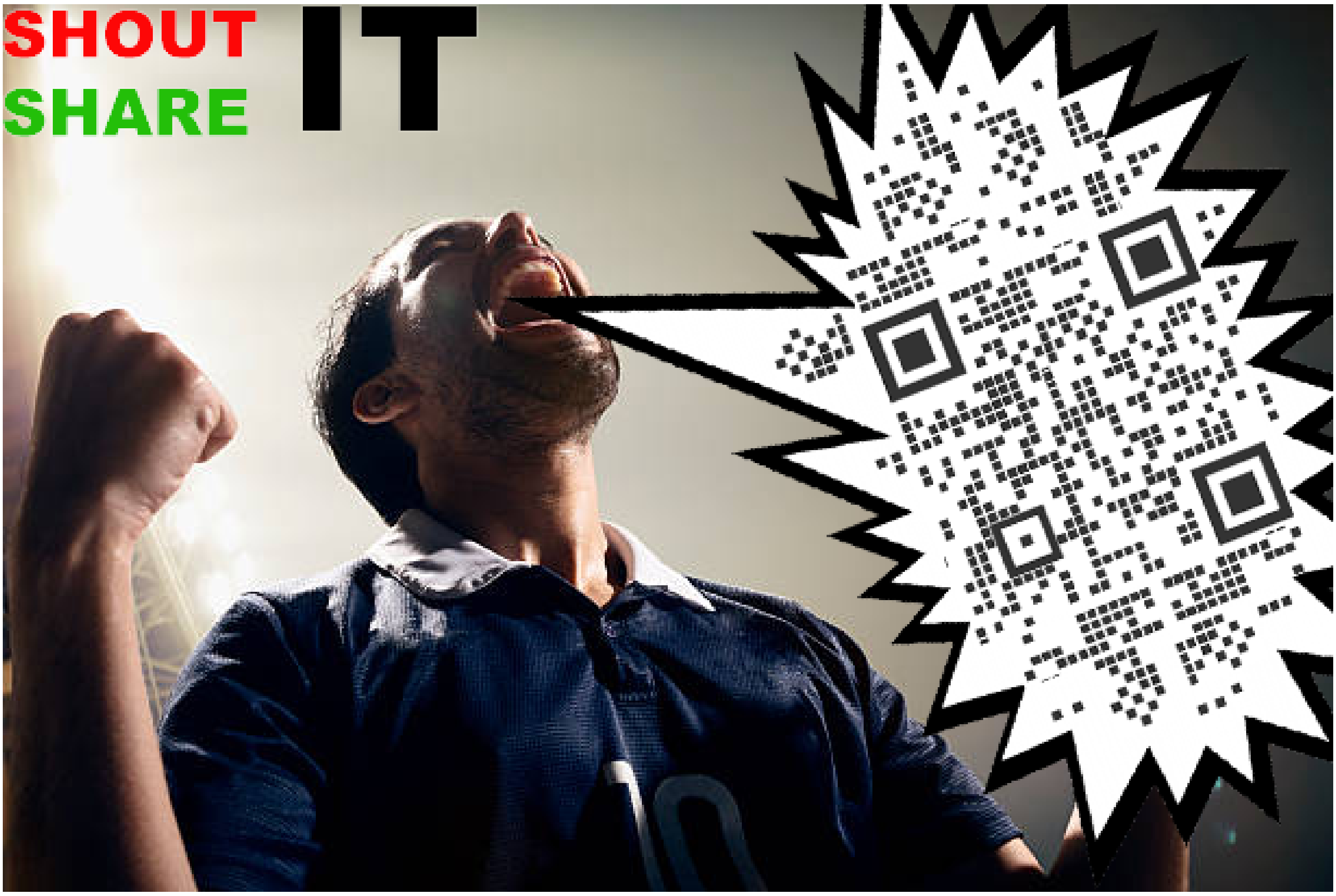
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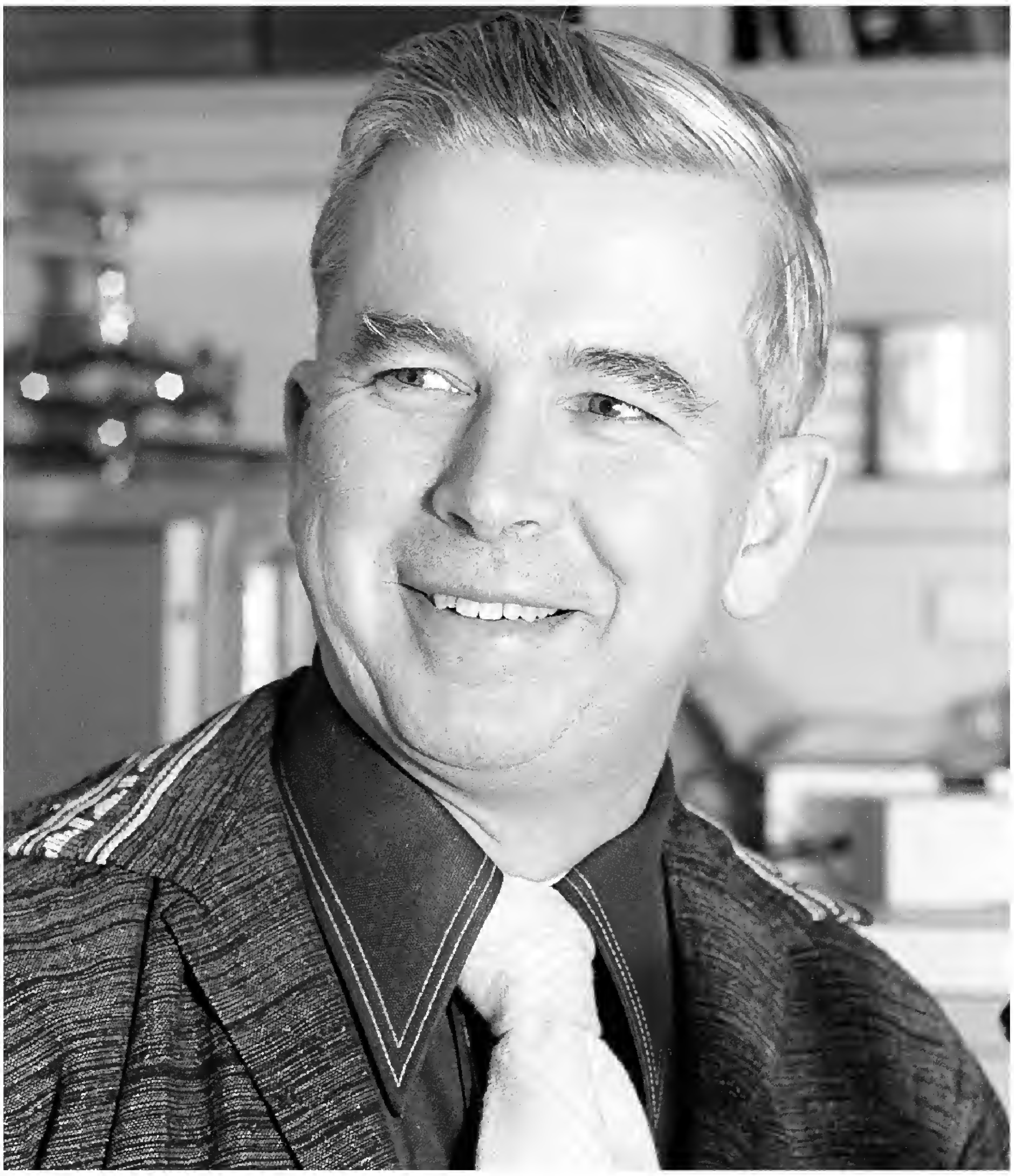

William Gerald D'Arcy
1931–1999

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1

FOREWORD

Thomas B. Croat

Bill D'Arcy and I met in 1969, just a little over two years after I had arrived at the Missouri Botanical Garden from the University of Kansas to begin my work with the *Flora of Barro Colorado Island*. We immediately found that we had a lot in common. Both of us had lived in the Virgin Islands for a short time, and both had a strong connection to the prairies of Saskatchewan. His family lived in Moose Jaw, not very far north of the village of Halbrite where my mother was born. We were also a bit older than most of the graduate students who worked in the alcoves hidden among the herbarium cases in the large, old three-story building that is now the administration building. Eventually we would both be involved in rehabbing old St. Louis housing so we would share tools, advice, and experiences. We became lifelong friends and would often share holiday occasions together since neither of us had family in St. Louis. We also dined out together with our wives, and this often involved nights of drinking and dancing at local places including one of our favorites, the riverboat Admiral, which had a marvelous 16-piece orchestra. Bill and my wife, Pat, were also close friends, and it was usually the two of them who made the social arrangements.

In 1970 Pat and I moved to Panama where I took up residence at Summit Gardens as the first Curator of Summit Herbarium (SCZ). While we were there, Bill came to study the Solanaceae of the country. He claimed he was going to purchase a motorcycle to collect with but I convinced him he would be better off using our field vehicle, which we had purchased for use in the *Flora of Panama* collecting program that had been reinitiated by Walter Lewis. I later regretted that I had encouraged him because he nearly drove the wheels off of it visiting many parts of Panama. He even rented a boat and traveled down part of the San Blas coast, on the basis of his theory that he would encounter unique plants there because of the influence of the indigenous people living in the region.

Bill was always full of ideas, and his fertile mind led him into many areas of investigation. His broad range of interests made him an interesting conversationalist. Any single discussion ranged from biology to politics, history, economics, and philosophy. I rarely agreed with him politically, but we argued happily and enjoyed each other's points of view.

This volume and the broad array of participants who have contributed papers for it demonstrate the esteem in which we held Bill D'Arcy and the friendship of the many people who came into his professional life. It is a pity that his life was cut short by cancer because he was such a prolific worker and truly loved what he was doing. Arriving late in his final career he worked at it seemingly ever harder. He proved to be a skilled manager, an excellent editor, and a linguist including French, Spanish, German, and Latin. He was also knowledgeable in the history of early explorers and the rules of nomenclature. He was my constant source of information from the trivial to the exact.

The 20 research contributions presented here cover a wide array of subject matter. For Solanaceae, aspects of the genera *Calibrachoa, Chamaesaracha, Deprea, Jaltomata, Larnax, Lycium, Metternichia, Petunia, Physalis*, *Sessea,* and *Solanum* are treated. Representing other families are *Anthurium* (Araceae), *Eugenia* (Myrtaceae), *Coffea, Gaertnera, Psilanthus* (Rubiaceae), and *Vepris* (Rutaceae). Thirteen new species are described within five families. The various character sets applied to systematic or evolutionary problems treat cytology, morphology, palynology, nectar secretion, and trichomes.

Nearly all of these approaches to evolutionary botany were in areas where Bill had at least some experience, and I know he would have enjoyed seeing these contributions immensely. For those who knew Bill well, it will be an opportunity to contemplate his career. For those who did not know him, it will be an opportunity to learn something about this remarkable man.

2

WILLIAM GERALD D'ARCY, 1931–1999: BIOGRAPHY, BIBLIOGRAPHY, PLANT TAXA NAMED BY HIM, AND PLANT TAXA NAMED IN HIS HONOR

Richard C. Keating

Abstract. William Gerald D'Arcy (1931–1999) was born in Calgary, Alberta, Canada, and he died in St. Louis, Missouri, at age 68. Although in his youth Bill D'Arcy showed early interest in natural history, as a young man he pursued a career in economics and business. As the owner-manager of a factory on the island of Tortola, British Virgin Islands, he became fascinated by the botany of the islands and finally decided to become a taxonomic botanist. He was accepted into the graduate program at the University of Florida where he obtained his master's degree under Dan Ward's direction. He continued graduate work at Washington University, St. Louis, where he worked under the guidance of Walter Lewis. His doctoral thesis, *The Solanaceae of Panama,* led to employment by the Missouri Botanical Garden where he managed the multi-volume *Flora of Panama* project to completion. His career at the garden, between 1972 and his death, included 25 field expeditions and his early emergence as a world expert on the classification and biology of the economically important plant family Solanaceae. D'Arcy's bibliography contains 144 publications on a variety of topics within and outside of his favorite specialty. Over his career he published 186 plant names. Twenty plant species have been named in his honor.

Key words: *bibliography, biography, D'Arcy, William Gerald, Flora, Panama, Solanaceae, plant taxonomy.*

William Gerald D'Arcy lived a diverse and colorful life, arriving at the practice of plant taxonomy relatively late and by a uniquely sinuous path. In addition, because of his entrepreneurial spirit and willingness to take chances, his life was punctuated by several failures and deep disappointments. But by dint of exceptional native abilities and intrinsic self-confidence he always recovered, and he carved out a distinguished career.

Bill was born on August 29, 1931, in Calgary, Alberta, Canada, where his father worked as a Claims Agent for the Canadian Pacific Railroad. Bill grew up in Moose Jaw, Saskatchewan, and in Calgary, where he attended public schools. The first of his life's twin themes, economics and natural history, emerged when he was about 10 years old and he led his school group in the sale of Canada War Bonds. His natural history interests developed during his high school years when he studied taxidermy and became a serious collector of bird eggs. The egg collection grew to over 200 properly mounted specimens and was donated to a local museum as a complete collection from all the breeding birds native to southern Alberta.

In an effort to raise money to support his youthful hobbies, Bill supplied moss, probably *Sphagnum*, to a local florist who used it for packing flowers. Pulling his brother's wagon, he would walk seven miles to a site he discovered on the Elbow River where he packed moss for sale at the then-lucrative return of $1 per potato bag.

In school Bill was an all-around good student except for Latin, an obvious prerequisite for his later calling. After his teacher ridiculed his poor performance one time too many, he vowed, "I'll show her." Forthwith he bore down every evening, obtaining the highest Latin scores ever in the Alberta School system for three years running.

More well-rounded than average, young Bill set up and used his own photographic darkroom, assembled a fine collection of Canadian postage stamps, edited the school paper, established a musical trio that played for school dances, and started the school chemistry club. Before heading for college, Bill joined the Reserve Officers Training Program of the army reserves. He played in the band, rose to the rank of captain, trained for the intelligence corps, and was selected for the Bisley Marksman Rifle Team.

In his freshman year at the University of Alberta, Bill was not an exceptional student as he discovered and took full advantage of social opportunities, joined a fraternity, and founded another trio to play at fraternity dances. For his second year, Bill changed majors from chemistry to economics as he became much more interested in money and the making of it. His desultory freshman performance changed to superior marks in his major and in the French language. For his junior year he won a prestigious National Federation of Canadian University Students scholarship to study economics at the University of Toronto.

In 1954, after receiving his B.A., he was selected to join an elite group for training as a member of the Canadian Foreign Trade Service in Ottawa. After learning Mandarin in preparation for posting to Hong Kong, he was instead assigned as deputy trade commissioner to Chicago. After two years in this profession he decided to seek his fortune by joining the commercial world, finding his first job as economist and vice president of Oppenheimer Sausage Casing Company in Chicago. In 1957 Bill and Jeanette J. Vaast were married. The couple moved to New York, where Bill worked as a vice president and economic analyst with the American Can Company on Fifth Avenue. Bill and Jeanette had two children, Charlotte and Lorraine.

At that time American Can Company provided subsidized holidays to resorts where employees and their families could totally relax. It so happened that their first such holiday was to Tortola in the British Virgin Islands, where Bill was immediately enchanted by the beauty of the place. Simultaneously, he was not happy with the New York corporate "rat race." Wheels began to turn in his mind and soon he resigned his job to become an entrepreneur on Tortola.

With financial help from his brother, Bill founded a company, bought a dormant soft drink factory, and believed he could overcome all the problems associated with labor and supplies availability on the islands. The business, "Tortola Pure Sparkling Water, 32 flavors," was a success at first. On Sunday, Bill's day off, the family would go to the beach where Bill soon became bored with beach culture. He took to examining the plants growing behind the dunes. As the business operated, Bill took time to collect plants while taking his truck around the island making soda pop deliveries.

As colleague Charlotte Taylor noted, at that time there was little serious shopping to be accomplished in the British Virgin Islands. For this, one traveled to Puerto Rico. There, the English-speaking and botanical communities were small enough that Bill met Roy Woodbury, for many years a botanist at the University of Puerto Rico, Río Piedras campus. Later, Roy was proud to take credit for having encouraged Bill to enter floristic botany.

Problems began to loom in paradise as it became clear that Bill's firm would not succeed. In addition, Bill and Jeanette realized that schooling would be limited for their daughters. Finally, an explosion at the factory sent a piece of steel into Bill's skull and nearly took his life. Surgery plus recuperation cost many months of inactivity during which Bill reevaluated his life's goals.

While winding down the business in preparation for selling it, Bill's travels on the island intensified his interest in the local flora. Using plant manuals from the library and a homemade plant dryer, he set about expanding his small herbarium collection. As suggested by Roy Woodbury, specimens he could not identify locally were sent off to several botanists and herbaria, including Richard Howard at the Arnold Arboretum and Dan Ward at the University of Florida. Bill also sent specimens to the University of Jamaica and to the Royal Botanic Gardens, Kew. All were impressed with the quality of his work, and Bill decided he had sufficient specimens and information to do a flora of Tortola. It became his first publication in 1967.

Concurrently, Richard Howard was working on a flora of the Lesser Antilles and was especially encouraging to Bill as he undertook his flora project. Much surviving correspondence suggests that Howard's patience and willingness to advise the young businessman were probably crucial to Bill's deciding to become a botanist. While he cast about for a graduate program, the University of Florida was sufficiently impressed with his past academic record to offer him a fellowship to pursue a master's degree in plant taxonomy.

So, in 1966, Bill packed up his wife and daughters and moved to Gainesville where the family lived in graduate student poverty. Working with Dan Ward, Bill finished his course requirements and his thesis on the taxonomy of *Solanum* in Florida within two years. His correspondence at that time indicates complete happiness with having been "bitten by the botany bug." In a sentiment not uncommon to those of us who stumble into systematic botany, he had written to Dick Howard, "I suppose I shall always be amazed that a refreshing pastime can pay for itself in full-time employment and training."

It was in 1968, Bill's final master's year, that Walter Lewis first learned of him. Lewis noted, "It is always a pleasure to receive a letter from a prospective student, especially when the inquiry is from an obviously mature person who has a clear focus of future intent and of the institutions being queried." Bill had singled out Washington University because of the Missouri Botanical Garden's expanded field research and station at Summit Gardens in Panama. Bill had learned of the program, fueled by Walter Lewis's several federal grants, that was designed to reinvigorate Woodson's *Flora of Panama* project. As Lewis stated, "This activity fit perfectly with his plan to work on tropical systematics and a broadened Solanaceae effort, as it did ours to complete the flora."

Bill enrolled at Washington University on January 29, 1969, and I met him soon after. His desk was adjacent to Duncan Porter's in a large room adjacent to the library in the old highceilinged administration building. Truly happy with his life, Bill pursued his work with good humor and energy. He was unfailingly interested in what I or other visitors had to contribute about things botanical. In May 1970 he passed his preliminary examination with excellence. By August 18, 1972, he had his Ph.D. in hand. Bill's thesis of 559 pages was entitled "The Solanaceae of Panama." It treated 20 solanaceous genera and their Panamanian species, accompanied by 73 plates of illustrations and maps. "He had found a Mecca in the American tropics for studying this family in what proved to be a lifelong passion," said Walter Lewis.

During this period Bill and Tom Croat became good friends as they shared common interests and a common Canadian background. For his thesis fieldwork, Bill made his first trips to Panama, where Tom Croat was botanist in charge of the *Flora of Panama* project and supervisor of Bill's collecting work. After obtaining his Ph.D. Bill, at 41, an age when many curators and academics have reached terminal promotion, finally began his career as a taxonomic botanist.

His experience with the Panamanian flora led to Bill's being granted a post-doctoral position at the Missouri Botanical Garden, and it evolved in time through Research Botanist into a Senior Curatorship. His continuing interest in education was reflected by his ongoing relationship with the Washington University Biology Department. He was appointed Lecturer in 1974, Faculty Associate in 1975, and finally Adjunct Professor in 1980. He also served as Associate Professor at the University of Missouri–St. Louis. During his career he was on the examination committees of two doctoral students: Richard Wunderlin, Saint Louis University, 1973, and David H. Lorence, Washington University, 1980. He worked closely with three master's students from the University of Missouri–St. Louis: Tilton S. Davis IV, 1975, John D. Judd, 1977, and Jane Stevens, 1990.

To begin his post-doc, Bill was given the task of preparing treatments for the *Flora of Panama*, which was being directed by Duncan Porter and later by Tom Croat. Soon Garden Director Peter Raven placed Bill in charge of completing the *Flora of Panama* project with a mandate to get it done with all feasible dispatch. Begun decades earlier by the late Robert Woodson, the *Flora* had been inching ponderously forward until 1965, when the first of Walter Lewis's several grants reestablished its priority. Over the 1970s, Bill made numerous trips to Panama, and he personally wrote many of the family and generic treatments for the *Flora*.

Much of his responsibility involved lining up other taxonomists to do treatments for the *Flora*, including the huge Compositae treatment to which he also contributed. Organizational skills gleaned from his government and business experience proved highly effective, although his insistence on meeting deadlines, rare at that time among academic taxonomists, cost him some friendships.

In the late 1970s dumb terminals and personal computers were just appearing and Bill was quick to realize their potential for managing floristic databases. Working with the mainframe computer center at the University of Missouri–St. Louis, Bill studied Turbo Pascal and wrote the data management software to produce the *Flora of Panama* index, the first flora in the world to be so treated. In under a decade Bill brought the enormous *Flora* project to completion. Treatments done under his direction, and the index, set a distinguished standard, still relevant as a model of the modern tropical flora.

To mark its completion, he organized the *Flora of Panama* symposium in collaboration with the Smithsonian Tropical Research Institute. The meeting, held in 1980 in Panama City, was superb and was attended by tropical biologists from throughout the hemisphere. Later Bill and his co-editor, Mireya M. Correa A., saw the proceedings to publication as *The Botany and Natural History of Panama*.

In 1975, in a fascinating diversion from the concerns of New World botany, Bill accepted an invitation from Dian Fossey to work for a year in Rwanda, Central Africa, on her mountain gorilla

Bill D'Arcy pressing a cultivated specimen of *Trevesia* from the Araliaceae family, 1979.

Bill in his office in the Lehmann Building at the Missouri Botanical Garden, 1982.

project. His assigned task was to probe the dietary habits of these gentle but huge and intimidating vegetarians. Early on he was initiated into the social mores of the primate world when, inadvertently, he got too close to a gorilla family group. He was quickly challenged and stood over by an angry old silverback who roared and beat his chest while Bill cowered on the ground in abject terror such as few humans ever live to recount.

Over months of work, rich experiences followed as Bill learned much Rwandan botany, tracking techniques, how to identify seeds from fecal remains, and of the many signs of the gorillas' profound influence on the ecology of their habitat. Then disaster struck. One day while leaving for the field, Bill left his hut with its fire-powered plant dryer in the hands of a negligent local field assistant. He returned to find his quarters and another building burned to the ground, including destruction of his accumulated voucher specimens, clothes, and passport. Since fire had threatened the entire camp, Ms. Fossey, unfairly in Bill's opinion, blamed him for the loss. He left the expedition distraught and severely set back.

As with his failed Tortola business venture, he rarely spoke of this disaster again. In spite of some later efforts, he could not bring himself to work up a publication on his observations.

On returning from Africa to St. Louis, Bill found himself alone and broke. He set about immediately to rectify the latter problem. At that time the city of St. Louis had a program of allowing people to buy condemned buildings for very little money and giving buyers six months to bring them up to code or face demolition. Earlier, using this opportunity, he had rehabilitated a house for his family. With a borrowed $1800 Bill purchased a four-unit apartment building in his Garden neighborhood and proceeded to spend his evenings and weekends tearing out walls, attending to wiring, plumbing, dry-walling, roofing, and foundation work. He managed to meet the city's deadline. Tom Croat, having similar talent and experience, was a dependable consultant. Within a year Bill had renters for these units. Then he repeated the process over the next several years with an eight-unit building. In those days he was intense, struggling to retain his usual sunny outlook. By good fortune Bill encountered Nancy Speed, a teacher in the St. Louis public schools who was assigned to the Missouri Botanical Garden's environmental education program. In October 1981 they were married, Bill sold his buildings, and they moved away from the Garden neighborhood. Bill and Nancy loved to go to restaurants all over the St. Louis area and usually sought out places where dancing was allowed. Sharing a love of travel among many other interests, they remained devoted to the end.

Bill's energy held forth unabated, and the late 1970s and 1980s were years of extraordinary scientific productivity. He published a long string of papers on the systematics of Solanaceae, rapidly becoming a top expert in this large and economically important family. He edited the *Solanaceae Newsletter*, served on steering committees for several international Solanaceae conferences, one of which he hosted. At one time Bill told me he submitted seven manuscripts within one week. As Walter Lewis noted, a few examples from Bill's large bibliography illustrate his expertise in the Solanaceae as well as other interests. For *Solanaceae: Biology and Systematics* (Columbia University Press, 1986), he edited the volume, contributed a major paper, and wrote introductions to parts of the book, such as Taxonomy and Biogeography, Comparative Chemistry, Origins and Distinctions of Domesticates, and The Human Interactions, all of which showed broad interests encompassing systematics and much more. It was a source of great satisfaction to him when *The Anther: Form, Function and Phylogeny*, co-edited by me, was published. "The first chapter by Bill, 'Anthers and Stamens and What They Do' says it all about male sex in plants," said Lewis.

Professional responsibilities at the Garden in the 1990s involved undertaking treatments of Solanaceae for the *Flora of China*, and for Madagascar. In 1993 he was assigned to take over the unfinished Bignoniaceae project left behind by the late Alwyn H. Gentry. He did this productively, writing an NSF grant, the funding of which allowed the hiring of post-doc Warren Hauk, a young botanist who brought a molecular background to the herbarium work in which he rapidly gained competence. Their success as a team led to a renewal of the grant around the time of Bill's death.

In the late 1990s, Bill developed prostate cancer which, within a year, he believed he had beaten with a combination of chemo and radiation therapy. Several months after being pronounced cancer-free, but still not at full strength, Bill traveled to Taiwan on a botanical visit to the field and herbaria. While in Taipei he realized he was ill again. Upon return to St. Louis, he was diagnosed with esophageal cancer that had apparently spread to his liver. He was given a year to live, which through love of life and focused drive extended to 18 months. Cared for at home by his wife, Nancy, Bill died on December 16, 1999.

From the beginning of our friendship, I was attracted to the fact that Bill had very broad concepts of what is appropriate scientific thinking for a systematist. Particularly we both wanted to know how adaptations worked and were not content merely to use them as "characters." Each week we would argue about such topics as pollinator reward systems, the role of calcium and calcium oxalate in the solanaceous blooming cycle, the origin of internodal branching in the Solanaceae, the unusual floral egress of the corolla in the family, and the nature of the scents produced by anthers. Often our arguments would send us to the library, or greenhouse, or in my case to the microtome, in an attempt to solve the problem. In some instances we co-authored manuscripts that had not been originally anticipated. Always, Bill would pull back from being drawn into more complex experimental procedures. As befits a good taxonomist, he stayed out of the red/far-red light district.

During the 1980s, as part of his ongoing strategy for avoiding poverty he sharpened up his original training in economics and became expert in managing investments. Over a hundred lunches, he held forth on the mysteries of P/E ratios, market volatility, calendric cycles, and forecasting stock performance from growth curves. He had total grasp of the psychology of investing and based on several instances I can say that his predictive capabilities were eerily on the mark.

For example, at the Berlin botanical congress in August of 1987, he casually remarked that he had moved his investments to cash. "Why?" I asked. "Well, you can see that the market average P/E ratios are unsustainable, the beta is too high in the manufacturing sector and the market is unstable. Watch for a serious correction soon." Then came October 19th and the Dow's 500-point drop. While others of us lost about 20% of our values, Bill picked the bargains and rode the market to new heights over the next several months. In another life he could have been a Peter Lynch.

Fortunately for botany, money took second place. Nancy and science were more powerful attractants. Over his short career Bill participated in 25 field expeditions and published about 144 contributions. He became expert in nomenclature and was a resource on several languages and older botanical literature.

Tom Croat put it well: "I can truthfully say that Bill D'Arcy was the most talented botanist I have ever known, being expert and knowledgeable in more fields and more different aspects of biology than any other person I have known. There are lots of people who might know more about a particular subject or a particular field but the breadth of his knowledge was truly amazing. To me he was a never-ending source of information which he gave freely and cordially."

Beloved by fellow Solanologists and by many students and colleagues, Bill was an open and loyal friend to a world of botanical sojourners.

ACKNOWLEDGMENTS

In addition to personal records and recollections, I am especially indebted to Nancy Speed D'Arcy, and to Bill's brother, Robert D'Arcy, for good stories and detailed notes regarding Bill's early years. Bill's mentor Walter Lewis offered key information and critical comments. Some of the notes were published by Lewis in *Biologue*, Newsletter of Washington University's Biology Department, 28 February 2000. The manuscript was enriched by colleagues Thomas Croat and Charlotte Taylor, who provided anecdotes and detailed comments as the manuscript progressed. Copies of correspondence between Bill and the late Richard Howard and notes from Dan Ward were very helpful. Original compilations of Bill D'Arcy's bibliography, and of plant taxa associated with him, were supplied by Jim Solomon, Robert Magill, and Kathy Hurlbert. I am particularly grateful to Victoria Hollowell and her assistant editors Amy McPherson and Diana Gunter for their able and patient labor as this volume progressed toward completion.

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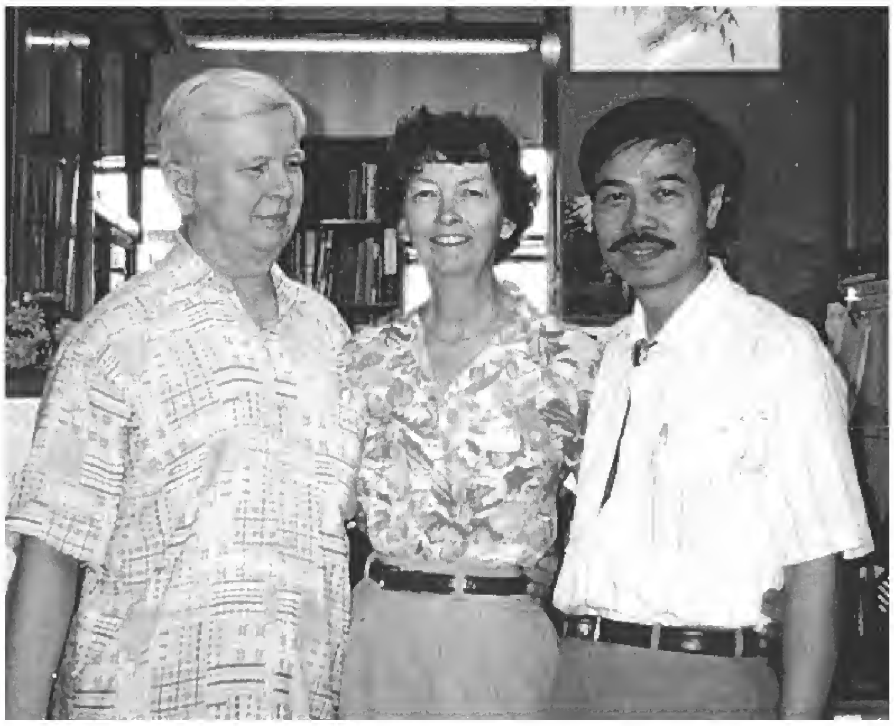
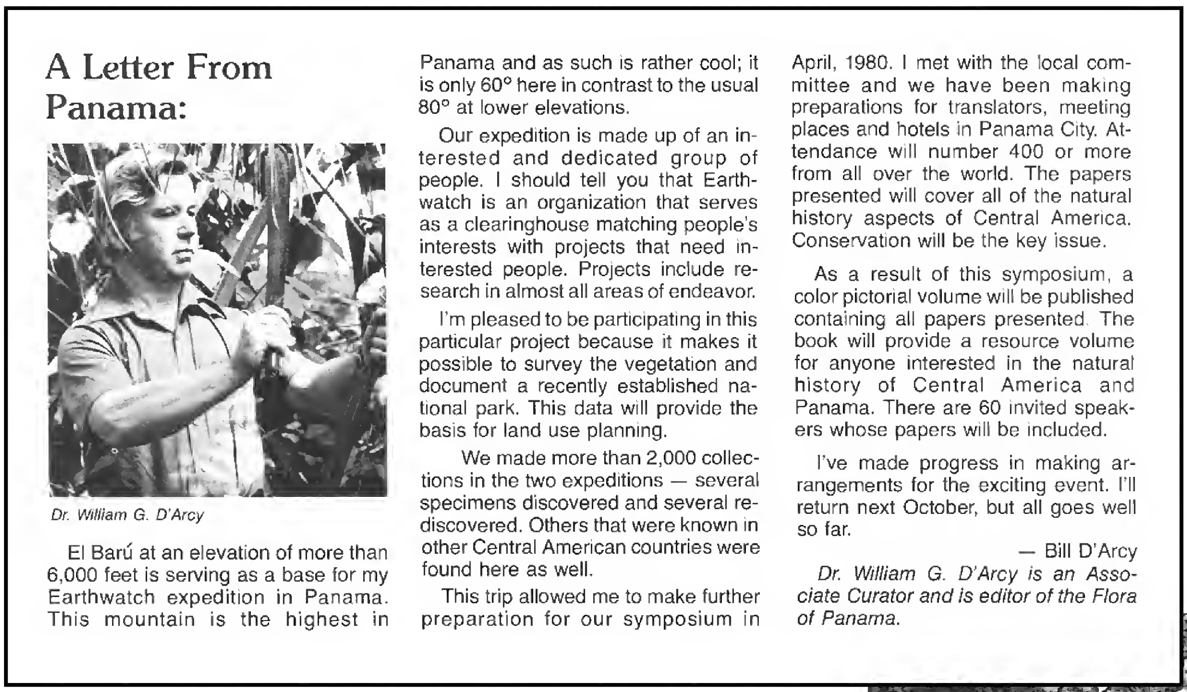
Left: Bill in Taiwan, 1998.

Below: Bill with Carmen Benítez de Rojas in his office at the Missouri Botanical Garden, 1995.



Above: Bill and Nancy D'Arcy with Ching-I-Peng in Taiwan, 1998.

Right: Bill with Dian Fossey, 1975.



A Letter From Panama:

Dr. William G. D'Arcy

El Barú at an elevation of more than 6,000 feet is serving as a base for my Earthwatch expedition in Panama. This mountain is the highest in Panama and as such is rather cool; it is only 60° here in contrast to the usual 80° at lower elevations.

Our expedition is made up of an interested and dedicated group of people. I should tell you that Earthwatch is an organization that serves as a clearinghouse matching people's interests with projects that need interested people. Projects include research in almost all areas of endeavor.

I'm pleased to be participating in this particular project because it makes it possible to survey the vegetation and document a recently established national park. This data will provide the basis for land use planning.

We made more than 2,000 collections in the two expeditions — several specimens discovered and several rediscovered. Others that were known in other Central American countries were found here as well.

This trip allowed me to make further preparation for our symposium in April, 1980. I met with the local committee and we have been making preparations for translators, meeting places and hotels in Panama City. Attendance will number 400 or more from all over the world. The papers presented will cover all of the natural history aspects of Central America. Conservation will be the key issue.

As a result of this symposium, a color pictorial volume will be published containing all papers presented. The book will provide a resource volume for anyone interested in the natural history of Central America and Panama. There are 60 invited speakers whose papers will be included.

I've made progress in making arrangements for the exciting event. I'll return next October, but all goes well so far.

— Bill D'Arcy

Dr. William G. D'Arcy is an Associate Curator and is editor of the Flora of Panama.

Left: From the Missouri Botanical Garden *Bulletin,* June–July 1979.

Below: Bill photographing a much sought-after Solanaceae.

BOEING 737-300

Left: Bill D'Arcy, Guanghua Zhu, and Tom Croat, 1993, in China.

Below: Taiwan, 1998. Over lunch, Bill briefed Professor Wang Jing-Ping, his assistant, and "Rich" (Yui-Ching Kiao) using xereox copies of specimens of the plants he hoped to see in the field.

REVISIONS
IN
SOLANACEAE

3

MAJOR CLADES IN *SOLANUM* BASED ON *ndh*F SEQUENCE DATA

Lynn Bohs

Abstract. Analysis of sequence data from the chloroplast gene *ndh*F identifies at least 12 major well-supported clades within the genus *Solanum.* These are briefly described, given informal clade names, and compared with the groups recognized by previous *Solanum* workers. Non-molecular synapomorphies are proposed for many of the clades. Continued use of informal taxonomic designations is advocated for new infrageneric groups within *Solanum.*

Key words: *ndh*F, phylogeny, Solanaceae, *Solanum*.

Solanum L., with approximately 1400 species, is the largest and most diverse genus in the Solanaceae. *Solanum* is distinguished from most of the other genera in the tribe Solaneae by its poricidal anther dehiscence, a character present in nearly all *Solanum* species and shared only with the related genus *Lycianthes.* Although some previous authors considered *Lycianthes* to be part of *Solanum,* recent molecular studies have confirmed the distinction between the two genera (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997; Olmstead et al., 1999). Morphologically, *Lycianthes* is differentiated from *Solanum* by differences in calyx structure (D'Arcy, 1986).

Although poricidal anther dehiscence is a relatively striking synapomorphy that allows *Solanum* to be recognized as a genus, its division into infrageneric subunits is less clear. Early workers attempted to divide *Solanum* into two large groups based on spininess, anther morphology, or hair type. Linnaeus, for instance, divided *Solanum* into two groups, *Spinosa* and *Inermia,* based on the presence or absence of spines (Linnaeus, 1753). Dunal, in his early treatments (Dunal, 1813, 1816), maintained this distinction as his categories *Aculeata* and *Inermia,* but in his *Solanum* treatment for DeCandolle's *Prodromus* (Dunal, 1852) he established two major infrageneric divisions ("sections") based on anther shape as well as presence or absence of spines. His group *Pachystemonum* encompassed species that lack spines and have relatively short, broad anthers with large terminal pores which often enlarge into longitudinal slits, whereas *Leptostemonum* included prickly species with relatively narrow, distally tapered anthers with small terminal pores that do not elongate with age. Bitter (1919) also recognized two major infrageneric groups, the subgenera *Eusolanum* and *Leptostemonum*, based on the same characters as Dunal (1852). Seithe (1962), in contrast, divided *Solanum* into two groups based not on spininess or anther morphology, but rather on hair type. She recognized two categories in *Solanum* at the rank of "Chorus subgenerum," distinguished by the presence of unbranched or dendritically branched hairs (Chorus subgenerum *Solanum*) versus stellate hairs (Chorus subgenerum *Stellatipilum*). Danert (1970) integrated characters of branching patterns and shoot morphology with previous systems, and, along with Gilli (1970), summarized the infrageneric groups recognized by Bitter and Seithe.

These works provided the elements of D'Arcy's (1972) classification scheme and conspectus, which is the most widely used system today.

TABLE 1.

Solanum subgenera according to D'Arcy (1972, 1991).

1. *Solanum* subg. *Archaesolanum* Marzell
   ca. 8 species, Australian region
2. *Solanum* subg. *Bassovia* (Aubl.) Bitter
   ca. 15 species, New World
3. *Solanum* subg. *Leptostemonum* (Dunal) Bitter
   ca. 250–450 species, worldwide
4. *Solanum* subg. *Lyciosolanum* Bitter
   1 species, South Africa
5. *Solanum* subg. *Minon* Raf. [subg. *Brevantherum* (Seithe) D'Arcy, in D'Arcy (1972)]
   ca. 70 species, New World
6. *Solanum* subg. *Potatoe* (G. Don) D'Arcy
   ca. 300 species, worldwide
7. *Solanum* subg. *Solanum*
   200 species, worldwide

D'Arcy's scheme recognizes seven subgenera in *Solanum* (Table 1; D'Arcy, 1972, 1991). These range in size from the monotypic subgenus *Lyciosolanum* to the subgenera *Solanum*, *Leptostemonum*, and *Potatoe*, each of which contains hundreds of species. In his 1972 paper, D'Arcy lectotypified all subgeneric names and provided a provisional conspectus of *Solanum*. In this conspectus, *Solanum* subgenera, sections, and series are listed along with their respective type species, but all the component species of each infrageneric group are not listed, nor are the characters given that circumscribe each of the groups. D'Arcy (1991) made minor modifications to this system. Whalen (1984) provided a detailed conspectus of *Solanum* subg. *Leptostemonum* (the spiny solanums). Subsequently, both Nee (1999) and Child and Lester (2001) provided infrageneric schemes for *Solanum*. Nee (1999) listed the species that belong to each of his taxonomic categories, but his system includes only New World taxa. Child and Lester (2001), like D'Arcy (1972), listed only the type species for each of their infrageneric groups. Hunziker (2001) modified D'Arcy's (1972) system and provided descriptions and commentary for each recognized section. All of these classifications relied completely on morphological data and, except for Whalen (1984), none utilized techniques of cladistic analysis.

The advent of molecular data has revolutionized the field of plant systematics and has led to new insights into phylogenetic relationships at all taxonomic levels. In the Solanaceae, Olmstead and colleagues have used restriction site and sequence data to examine phylogenetic relationships across the entire family (Olmstead & Palmer, 1992; Olmstead et al., 1999). Molecular studies above the sectional level in *Solanum* include the works of Spooner et al. (1993), Olmstead and Palmer (1997), and Bohs and Olmstead (1997, 1999, 2001). These studies provide information on major clades within *Solanum*, but none have sampled from all the subgenera recognized by morphological systematists such as Bitter, Seithe, Danert, and D'Arcy.

This paper presents results of a molecular phylogenetic study designed to identify major clades within *Solanum* using sampling from a broad spectrum of *Solanum* subgroups. Results are presented from an analysis of sequence data from the chloroplast gene *ndh*F. Sampling includes members of all seven of D'Arcy's subgenera and over 40 of the 62 sections listed in D'Arcy (1991). All the sections listed in D'Arcy's (1972) conspectus as well as many sections described after 1972 are discussed in context of the major *ndh*F clades. Major lineages are described with informal clade names and their component sectional groups are listed. Possible non-molecular synapomorphies are suggested for most of the identified clades. These characters have been taken from the general references listed above and from the personal observations of the author. Although they may provide general guidelines for the recognition of clades, this is not intended to be a substitute for thorough morphological analyses, as many of the suggested characters are variable within clades and may be found in more than one clade. A few overall recommendations are made for taxonomic rearrangements within the genus *Solanum*. Results of analyses using data from nuclear genes such as ITS and *waxy* (Bohs, in prep.) and from combined chloroplast and nuclear sequence data sets will be presented in a future publication.

MATERIALS AND METHODS

Sampling comprised 120 species of Solanaceae, including five outgroup genera from the tribe Solaneae. Outgroup taxa were chosen on the basis of previously published results of Olmstead et al. (1999) and Bohs and Olmstead (2001). *Solanum* taxa sampled included representatives of all seven of D'Arcy's subgenera and a number of sections or species groups thought to represent distinctive clades based on morphology. Collection and voucher information is given in Table 2.

DNA was extracted from fresh or silica-dried leaves or, in rare cases, from herbarium specimens, using either the modified CTAB procedure of Doyle and Doyle (1987) or a microextraction protocol that used QiaQuick columns and buffer (Qiagen, Inc.) in place of the isopropanol precipitation step in the CTAB procedure. Samples

TABLE 2.

Sources of taxa sequenced for *ndh*F. [a]DNA extracts provided by: (1) L. Bohs, University of Utah, Salt Lake City, Utah; (2) R. G. Olmstead, University of Washington, Seattle, Washington; (3) T. Mione, Central Connecticut State University, New Britain, Connecticut; (4) D. Spooner, University of Wisconsin, Madison, Wisconsin; (5) A. Bruneau, McGill University, Montreal, Canada. [b]According to D'Arcy (1972, 1991) unless noted. [c]Accession numbers given for cultivated collections. BIRM = cultivated at University of Birmingham, U.K.; NIJ = cultivated at University of Nijmegen, The Netherlands; PI = U.S.D.A. Plant Introduction number; D'Arcy collection = cultivated at MO. [d]Collector, number, and herbarium acronym (if known) of herbarium vouchers. [e]Child (1998). [f]Bohs (1990). [g]Nee (1999). [h]Symon (1981). [i]D'Arcy (1992). [j]Knapp (2000).

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Capsicum baccatum L. var. *pendulum* (Willd.) Eshbaugh[2]			Bolivia	*Eshbaugh 1584* (MU)	U08916
Capsicum chacoense Hunz.[2]			Bolivia	*Eshbaugh 1586A* (MU)	AF500809
Jaltomata procumbens (Cav.) J. L. Gentry[3]			Mexico	*Davis 1189A*	U47429
Jaltomata sinuosa (Miers) Mione[1]			Bolivia	*Nee et al. 51830* (NY)	AF500835
Lycianthes heteroclita (Sendtn.) Bitter[1]			Costa Rica	*Bohs 2376* (UT)	U72756
Lycianthes rantonnei (Carrière) Bitter[2]			BIRM S.0928	*RGO S-96* (WTU)	AF500840
Physalis alkekengi L.[2]			D'Arcy collection	*D'Arcy 17707* (MO)	U08927
Solanum abutiloides (Griseb.) Bitter & Lillo[2]	*Minon*	*Brevantherum*	BIRM S.0655	*RGO S-73* (WTU)	U47415
Solanum accrescens Standl. & C. V. Morton[1]	*Leptostemonum*	*Erythrotrichum*[e]	Costa Rica	*Bohs 2556* (UT)	AF500795
Solanum adhaerens Roem. & Schult.[1]	*Leptostemonum*	*Micracantha*	Costa Rica	*Bohs 2473* (UT)	AF224061
Solanum adscendens Sendtn.[1]	*Solanum*	*Gonatotrichum*	Bolivia	*Bohs & Nee 2738* (UT)	AF500796
Solanum aethiopicum L.[2]	*Leptostemonum*	*Oliganthes*	BIRM S.0344	*RGO S-74* (WTU)	AF500797
Solanum aggregatum Jacq.[2]	*Lyciosolanum*	*Lyciosolanum*	South Africa	*RGO 99-25* (WTU)	AF500798
Solanum aligerum Schltdl.[1]	*Minon*	*Holophylla*	Bolivia	*Nee et al. 51822* (NY)	AF500799
Solanum allophyllum (Miers) Standl.[1]	None[f]	*Allophyllum*[f]	Panama	*Bohs 2339* (UT)	U47416
Solanum amygdalifolium Steud.[1]	*Potatoe*	*Jasminosolanum*	Argentina	*Nee & Bohs 50840* (NY)	AF500800
Solanum aphyodendron S. Knapp[2]	*Solanum*	*Geminata*	Colombia	*RGO S-92* (WTU)	AF500801
Solanum appendiculatum Dunal[2]	*Potatoe*	*Basarthrum*	Mexico	*Anderson 1401* (CONN)	AF224062
Solanum arboreum Dunal[1]	*Solanum*	*Geminata*	Costa Rica	*Bohs 2521* (UT)	U47417

Solanum argentinum Bitter & Lillo[1]	*Minon*	*Holophylla*	Argentina	*Bohs 2539* (UT)	U72752
Solanum aviculare G. Forst.[2]	*Archaesolanum*	*Archaesolanum*	BIRM S.0809	none	U47418
Solanum betaceum Cav.[1]	Genus *Cyphomandra*	*Pachyphylla*	Bolivia	*Bohs 2468* (UT)	U47428
Solanum brevicaule Bitter[4]	*Potatoe*	*Petota*	Bolivia PI 498115	*Hawkes et al. 6701*	AF500803
Solanum bulbocastanum Dunal[4]	*Potatoe*	*Petota*	Mexico PI 347757	*Tarn 153*	AF500804
Solanum caesium Griseb.[1]	*Solanum*	*Solanum*	Bolivia	*Bohs et al. 2815* (UT)	AF500805
Solanum calileguae Cabrera[1]	*Solanum*[g]	*Dulcamara*[g]	Argentina	*Nee & Bohs 50809* (NY)	AF500806
Solanum campanulatum R. Br.[2]	*Leptostemonum*	*Campanulata*	BIRM S.0387	*RGO S-78* (WTU)	AF500807
Solanum campechiense L.[1]	*Leptostemonum*	Unclear	Costa Rica	*Bohs 2536* (UT)	AF224071
Solanum candidum Lindl.[2]	*Leptostemonum*	*Lasiocarpa*	BIRM S.0975	*RGO S-100* (WTU)	AF224072
Solanum capsicoides All.[1]	*Leptostemonum*	*Acanthophora*	Peru	*Bohs 2451* (UT)	AF500808
Solanum carolinense L.[2]	*Leptostemonum*	*Lathyrocarpum*	BIRM S.1816	*RGO S-77* (WTU)	AF500811
Solanum chenopodinum F. Muell.[2]	*Leptostemonum*	*Graciliflora*	BIRM S.0813	none	AF500812
Solanum cinereum R. Br.[1]	*Leptostemonum*	*Melongena*[h]	NIJ 904750120	*Bohs 2852* (UT)	AF500813
Solanum citrullifolium A. Braun[2]	*Leptostemonum*	*Androceras*	BIRM S.0127	*RGO S-79* (WTU)	AF500814
Solanum cleistogamum Symon[2]	*Leptostemonum*	*Oliganthes*	BIRM S.0844	*RGO S-80* (WTU)	AF500815
Solanum conditum C. V. Morton[1]	*Leptostemonum*	Unclear	Bolivia	*Bohs & Nee 2733* (NY)	AF500816
Solanum cordovense Sessé & Moç.[1]	*Minon*	*Extensum*	Costa Rica	*Bohs 2693* (UT)	U72751
Solanum crinitipes Dunal[2]	*Leptostemonum*	*Torva*	Colombia	*RGO S-81* (WTU)	AF500817
Solanum crinitum Lam.[1]	*Leptostemonum*	*Crinitum*[e]	NIJ 924750049	*Bohs 2850* (UT)	AF500818
Solanum crispum Ruiz & Pav.[2]	*Minon*	*Holophylla*	BIRM S.0486	none	AF500819
Solanum deflexum Greenm.[1]	*Solanum*	*Gonatotrichum*	Costa Rica	*Bohs 2715* (UT)	AF500820
Solanum delitescens C. V. Morton[1]	*Minon*	*Holophylla*	Argentina	*Nee & Bohs 50810* (NY)	AF500821
Solanum diploconos (Mart.) Bohs[1]	Genus *Cyphomandra*	*Pachyphylla*	Brazil	*Bohs 2335* (UT)	AY049014
Solanum doddsii Correll[4]	*Potatoe*	*Petota*	Bolivia	*Spooner et al. 6651*	AF500822
Solanum drymophilum O. E. Schulz[1]	*Leptostemonum*	*Persicariae*	Puerto Rico	*Bohs 2461* (UT)	AF500823
Solanum dulcamara L.[2]	*Potatoe*	*Dulcamara*	U.S.A.	none	U47419
Solanum echinatum R. Br.[1]	*Leptostemonum*	*Leprophora*	NIJ 954750052	*Bohs 2727* (UT)	AF500824
Solanum elaeagnifolium Cav.[2]	*Leptostemonum*	*Leprophora*	U.S.A.	*RGO S-82* (WTU)	AF224067
Solanum etuberosum Lindl.[4]	*Potatoe*	*Petota*	Chile PI 498311	*UAC 1322*	AF500825

Table 2 continued.

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Solanum evolvulifolium Greenm.[1]	*Bassovia*	*Herpystichum*[g]	Panama	*Knapp & Mallet 9178* (BM)	AF500826
Solanum ferocissimum Lindl.[2]	*Leptostemonum*	*Graciliflora*	BIRM S.0819	*RGO S-83* (WTU)	AF500827
Solanum fiebrigii Bitter[1]	*Solanum*	*Solanum*	Bolivia	*Bohs et al. 2784* (UT)	AF500828
Solanum fraxinifolium Dunal[1]	*Potatoe*	*Basarthrum*	Costa Rica	*Bohs 2558* (UT)	AF500810
Solanum furfuraceum R. Br.[2]	*Leptostemonum*	Unclear	BIRM S.1442	*RGO S-84* (WTU)	AF500829
Solanum glaucophyllum Desf.[2]	*Solanum*	*Glaucophyllum*	D'Arcy collection	none	U72753
Solanum havanense Jacq.[1]	*Solanum*	*Diamonon*[e]	NIJ 904750122	*Bohs 3076* (UT)	AF500830
Solanum herculeum Bohs[2]	genus *Triguera*		Morocco	*Jury 13742* (RNG)	AF224065
Solanum hindsianum Benth.[1]	*Leptostemonum*	Unclear	Mexico	*Bohs 2975* (UT)	AF500831
Solanum hoehnei C. V. Morton[1]	*Leptostemonum*	*Nemorense*	Brazil	*Folli 1668* (MO)	AF500832
Solanum inelegans Rusby[1]	*Minon*	*Holophylla*	Bolivia	*Nee et al. 51813* (NY)	AF500833
Solanum ipomoeoides Chodat & Hassl.[1]	*Solanum*[g]	*Dulcamara*[g]	Bolivia	*Bohs & Nee 2766* (UT)	AF500834
Solanum jamaicense Mill.[2]	*Leptostemonum*	*Eriophylla*	BIRM S.1209	*RGO S-85* (WTU)	AF224073
Solanum jasminoides Paxton[2]	*Potatoe*	*Jasminosolanum*	Colombia	*RGO S-86* (WTU)	AF500836
Solanum juglandifolium Dunal[4]	*Potatoe*	*Petota*	Colombia	LA 2788	AF500837
Solanum laciniatum Aiton[1]	*Archaesolanum*	*Archaesolanum*	New Zealand	*Bohs 2528* (UT)	U47420
Solanum lepidotum Dunal[1]	*Minon*	*Lepidotum*	Costa Rica	*Bohs 2621* (UT)	AF500838
Solanum lidii Sunding[1]	*Leptostemonum*	*Nycterium*	NIJ 934750022	*Bohs 2903* (UT)	AF500839
Solanum luteoalbum Pers.[1]	Genus *Cyphomandra*	*Cyphomandropsis*	BIRM S.0042	*Bohs 2337* (UT)	U72749
Solanum lycopersicum L.[2]	Genus *Lycopersicon*	*Lycopersicon*	U.S.A. (cult.)	none	U08921
Solanum macrocarpon L.[2]	*Leptostemonum*	*Melongena*	BIRM S.0133	*RGO S-88* (WTU)	AF224068
Solanum mahoriense D'Arcy & Rakot.[1]	*Leptostemonum*	*Cryptocarpum*[i]	Madagascar	*Bohs 2576* (UT)	AF500841
Solanum mammosum L.[2]	*Leptostemonum*	*Acanthophora*	BIRM S.0983	*RGO S-89* (WTU)	AF224074
Solanum mapiriense Bitter[1]	None[f]	*Allophyllum*[f]	Bolivia	*Nee & Solomon 30305* (UT)	AF500842
Solanum mauritianum Scop.[2]	*Minon*	*Brevantherum*	BIRM S.0860	*RGO S-90* (WTU)	AF500843

Solanum melongena L.[2]	*Leptostemonum*	*Melongena*	BIRM S.0657	*RGO S-91* (WTU)	AF224069
Solanum montanum L.[1]	*Potatoe*	*Regmandra*	NIJ 904750205	*Bohs 2870* (UT)	AF500844
Solanum multifidum Ruiz & Pav.[1]	*Potatoe*	*Regmandra*	NIJ 904750205	*Bohs 2863* (UT)	AF500845
Solanum muricatum Aiton[2]	*Potatoe*	*Basarthrum*	Colombia	*RGO S-93* (WTU)	AF500846
Solanum nemorense Dunal[1]	*Leptostemonum*	*Nemorense*	Bolivia	*Bohs & Nee 2757* (UT)	AF500847
Solanum nitidum Ruiz & Pav.[1]	*Minon*	*Holophylla*	Bolivia	*Nee 31944* (NY)	AF224075
Solanum ochrophyllum Van Heurck & Müll. Arg.[1]	*Solanum*	*Geminata*	Bolivia	*Bohs & Nee 2805* (UT)	AF500848
Solanum palitans C. V. Morton[1]	*Solanum*	*Parasolanum*	BIRM S.0837/70	*Bohs 2449* (UT)	AF224064
Solanum phaseoloides Pol.[1]	*Bassovia*	*Herpystichum*	Costa Rica	*Bohs 2485* (UT)	AF500849
Solanum physalifolium Rusby var. *nitidibaccatum* (Bitter) Edmonds[1]	*Solanum*	*Solanum*	U.S.A.	*Bohs 2467* (UT)	U47421
Solanum pinnatisectum Dunal[4]	*Potatoe*	*Petota*	Mexico PI 347766	*Tarn 205A*	AF500850
Solanum piurae Bitter[4]	*Potatoe*	*Petota*	Peru PI 310997	*Hawkes 2443*	AF500851
Solanum prinophyllum Dunal[1]	*Leptostemonum*	*Oliganthes*[h]	NIJ 904750171	*Bohs 2725* (UT)	AF500852
Solanum pseudocapsicum L.[2]	*Minon*	*Pseudocapsicum*	BIRM S.0870	none	U47422
Solanum ptychanthum Dunal[2]	*Solanum*	*Solanum*	U.S.A.	*RGO S-94* (WTU)	U47423
Solanum pubigerum Dunal[1]	*Minon*	*Holophylla*	NIJ 904750104	none	AF500853
Solanum pyracanthum Lam.[2]	*Leptostemonum*	*Oliganthes*	cult. (UCSB Bot. Gard.)	*RGO S-95* (WTU)	AF500854
Solanum quadrangulare L.f.[2]	*Solanum*	*Quadrangulare*	South Africa	*RGO 99-46* (WTU)	AF500855
Solanum riojense Bitter[1]	*Solanum*	*Episarcophyllum*	Argentina	*Nee & Bohs 50843* (NY)	AF500856
Solanum rostratum Dunal[1]	*Leptostemonum*	*Androceras*	U.S.A.	none	U47424
Solanum rovirosanum Donn. Sm.[1]	*Solanum*	*Geminata*	Costa Rica	*Bohs 2919* (UT)	AF500857
Solanum rugosum Dunal[1]	*Minon*	*Brevantherum*	Costa Rica	*Bohs 3011* (UT)	AF500858
Solanum sandwicense Hook. & Arn.[1]	*Leptostemonum*	*Irenosolanum*	Hawaii	*Bohs 2992* (UT)	AF500859
Solanum schimperianum Hochst.[2]	*Leptostemonum*	*Torva*	BIRM S.1538	*RGO S-97* (WTU)	AF500860
Solanum schlechtendalianum Walp.[1]	*Minon*	*Extensum*	Costa Rica	*Bohs 2915* (UT)	AF500861
Solanum seaforthianum Andrews[2]	*Potatoe*	*Jasminosolanum*	BIRM S.0051	none	U47425
Solanum sisymbriifolium Lam.[1]	*Leptostemonum*	*Cryptocarpum*	Argentina	*Bohs 2533* (UT)	AF500862
Solanum stenophyllidium Bitter[1]	*Potatoe*	*Petota*	NIJ 904750079	*Bohs 2855* (UT)	AF500802
Solanum stramonifolium Jacq.[5]	*Leptostemonum*	*Lasiocarpa*	Peru	*Whalen 860* (HUT)	AF500863

TABLE 2 CONTINUED.

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Solanum terminale Forssk.[1]	*Solanum*	*Afrosolanum*	NIJ 814750072	*Bohs 2719* (UT)	AF500864
Solanum thelopodium Sendtn.[1]	Unclear[j]	Unclear[j]	Bolivia	*Nee & Bohs 50858* (NY)	AF500865
Solanum toliaraea D'Arcy & Rakot.[1]	*Leptostemonum*	Unclear[i]	Madagascar	*Bohs 2574* (UT)	AF500866
Solanum torvum Sw.[2]	*Leptostemonum*	*Torva*	BIRM S.0839	*RGO S-101* (WTU)	L76286
Solanum tridynamum Dunal[2]	*Leptostemonum*	*Nycterium*	BIRM S.1831	*RGO S-102* (WTU)	AF500867
Solanum triflorum Nutt.[1]	*Solanum*	*Parasolanum*	U.S.A.	*Bohs 3062* (UT)	AF500868
Solanum tripartitum Dunal[1]	*Solanum*	*Parasolanum*	BIRM S.0708/71	*Bohs 2465* (UT)	U72750
Solanum trisectum Dunal[1]	*Potatoe*	*Normania*	France	*Bohs 2718* (UT)	AF224063
Solanum trizygum Bitter[1]	*Bassovia*	*Pteroidea*	Costa Rica	*Bohs 2511* (UT)	U72754
Solanum tuberosum L.[2]	*Potatoe*	*Petota*	U.S.A. (cult.) PI (245793 X 245796)	WRF 1610 USDA NRSP-6	L76287
Solanum turneroides Chodat[1]	*Solanum*	*Gonatotrichum*	Bolivia	*Nee et al. 51716* (NY)	AF500869
Solanum uleanum Bitter[1]	*Bassovia*	*Pteroidea*	D'Arcy collection	*Bohs 2720* (UT)	AF500870
Solanum vespertilio Aiton[2]	*Leptostemonum*	*Nycterium*	BIRM S.2091	*RGO S-103* (WTU)	AF224070
Solanum villosum Mill.[1]	*Solanum*	*Solanum*	Iran PI 304600	*Bohs 2553* (UT)	AF224066
Solanum wallacei (A. Gray) Parish[1]	*Potatoe*[e]	*Californisolanum*[e]	U.S.A.	*Bohs 2438* (UT)	U47426
Solanum wendlandii Hook. f.[2]	*Leptostemonum*	*Aculeigerum*	BIRM S.0488	none	U47427
Witheringia solanacea L'Hér.[1]			Costa Rica	*Bohs 2416* (UT)	U72755

extracted with the modified CTAB method were purified using cesium chloride density gradient centrifugation or a phenol-chloroform protocol. Amplification and sequencing of the *ndh*F gene used the primers and PCR program given in Bohs and Olmstead (1997). PCR products were cleaned using QiaQuick spin columns and sequenced on an ABI automated sequencer. Sequences were edited and contigs assembled using the program Sequencher (Gene Codes Corp.). After a consensus sequence was obtained, it was aligned by eye to a template sequence (*Nicotiana tabacum* L.). Base changes relative to the template sequence were then double-checked against the chromatograms. No alignment difficulties were encountered in assembling the sequences into a data set in NEXUS file format. All new sequences reported here have been submitted to GenBank (Table 2). The data set and resultant phylogenetic trees have been submitted to TreeBASE (accession numbers S735 and M1167).

The data matrix was analyzed using unweighted parsimony with the program PAUP*4.0b10 (Swofford, 2002). The analysis used the heuristic search algorithm with the TBR and MulTrees options, 714 random addition replicates with rearrangements limited to 100,000 per replicate, and gaps treated as missing data. Trees were rooted using *Physalis alkekengi* as the outgroup. Bootstrap analyses were performed with 500 replicates using the heuristic search option, TBR and MulTrees, MaxTrees set to 1000, and 1,000,000 rearrangements per replicate.

The data were also analyzed using the parsimony ratchet (Nixon, 1999) as implemented in the program PAUPRat (Sikes & Lewis, 2001). Five replicate searches of 200 iterations each were performed. The shortest trees from all searches were retained and combined into a single consensus tree.

The same data matrix was analyzed by maximum likelihood using the program fastDNAml (Olsen et al., 1994) on a UNIX platform computer. Parameters used in the analysis were a transition/transversion ratio of 1.0006 (estimated using ML in PAUP from a neighbor-joining tree of the 120-taxon data set), empirical base frequencies (A = 0.27665, C = 0.15518, G = 0.18366, T = 0.38450), and random addition order.

RESULTS

The *ndh*F sequences obtained for all taxa except *Lycianthes heteroclita*, *Solanum wendlandii*, *S. diploconos*, and *S. deflexum* were 2086 base pairs long, corresponding to positions 24 through 2109 in the tobacco *ndh*F sequence. *Lycianthes heteroclita* had a 15 bp insertion, *S. wendlandii* had a 33 bp insertion, and *S. diploconos* had a 24 bp insertion between positions 1476 and 1477. *Solanum deflexum* had a 9 bp deletion between positions 1703 and 1711.

Of 2119 total characters in the data set, 541 were variable and 288 of these were parsimony-informative. Pairwise sequence divergence calculated using the Kimura 2-parameter model ranged from 3.4% between *S. candidum* versus *Lycianthes heteroclita* to 0.048% in the closely related species pairs *S. ferocissimum* versus *S. chenopodinum*, *S. vespertilio* versus *S. liddii*, *S. doddsii* versus *S. stenophyllidium*, and *S. piurae* versus *S. doddsii*. *Solanum schlechtendalianum* and *S. lepidotum* had identical *ndh*F sequences.

The available memory capacity of PAUP on a Power Macintosh G4 was reached after saving 18,200 most parsimonious trees from 714 random addition replicates. These trees were 1053 steps long with a CI (excluding uninformative characters) of 0.497 and RI of 0.819. PAUPRat saved 992 trees of 1053 steps out of 1000 iterations. The strict consensus trees from the heuristic parsimony and the PAUPRat searches were nearly identical, differing only in greater resolution at two of the branch tips in the PAUPRat consensus tree (not shown). Likewise, the maximum likelihood topology (not shown) was virtually identical to the parsimony trees and included the same taxa in the major clades described below. This analysis was completed overnight, examined 39,626 trees, and resulted in a tree with a log likelihood of –13487.40739.

In these trees, *Solanum* forms a monophyletic clade, with members of the former genera *Lycopersion*, *Cyphomandra*, *Normania*, and *Triguera* nested within it (Fig. 1). Species of all these genera have been transferred to *Solanum* (Spooner et al., 1993; Bohs, 1995; Bohs & Olmstead, 2001). *Capsicum* plus *Lycianthes* emerges as the sister group to the *Solanum* clade with bootstrap support of 70%. *Solanum* plus the genera *Jaltomata*, *Lycianthes*, and *Capsicum* form a well-supported clade (bootstrap = 100%), and *Lycianthes* plus *Capsicum* form a well-supported group (bootstrap = 89%).

At least 12 major clades can be discerned within *Solanum* (Fig. 1, see pp. 48–49). These clades are supported with bootstrap values ranging from 51% (Leptostemonum s.l.) to 100% (the Regmandra, Archaesolanum, and Normania clades). However, the relationships among these major clades are unclear, because for the most part they form a polytomy at the base of *Solanum*. Several of these clades conform to infrageneric groups recognized by previous systematists, but others do not.

These clades have been given informal clade names and are briefly described below with a list of their constituent sections and non-molecular synapomorphies that may define them. Asterisks (*) indicate sections or species groups that have been sampled in the present analysis. Other groups listed under each clade are inferred to belong there due to morphological similarity. Brief comparisons are made with reference to D'Arcy's (1972) classification and with several other schemes.

DISCUSSION

Major clades defined by *ndh*F data:

1. Thelopodium clade

3 spp., South America

Included taxa:

Solanum thelopodium species group *sensu* Knapp (2000)*

This group is morphologically distinctive due to its enlarged roots, single-stemmed growth habit, reduced number of sympodia, and narrow, tapered, dimorphic anthers. It was revised recently by Knapp (2000), who recognized three species. One of them, *S. thelopodium*, was included in the *ndh*F analysis, where it forms a single branch at the very base of *Solanum*. This placement is surprising and has not been suggested by recent Solanaceae systematists, although Bitter thought that *S. thelopodium* was sufficiently distinct to merit generic rank (Knapp, 2000). Dunal (1852) and Seithe (1962) placed *S. thelopodium* into *Solanum* sect. *Anthoresis* (Dunal) Bitter, but this means little, as section *Anthoresis* is a catch-all group of disparate taxa. D'Arcy did not include it in either of his summary classifications (D'Arcy, 1972, 1991). Nee (1999) put this species into *Solanum* sect. *Pteroidea* (Potato clade), but the *ndh*F data do not support this placement. Further sampling is needed to determine if the basal position of this clade in *Solanum* is correct or is perhaps a long branch artifact.

2. Regmandra clade

ca. 7 spp., South America

Included taxa:

Solanum subg. *Potatoe* (G. Don) D'Arcy pro parte

Solanum sect. *Regmandra* (Dunal) D'Arcy*

D'Arcy (1972, 1991) placed this small group of species from Pacific coastal deserts of South America into *Solanum* subg. *Potatoe*. Nee (1999) also allied this section with the potatoes, whereas Child and Lester (2001) put it into *Solanum* subg. *Solanum*, and Hunziker (2001) considered its subgeneric position uncertain. Taxa of *Solanum* sect. *Regmandra* included in the *ndh*F data set are *S. montanum* and *S. multifidum*, and they fall out together on a well-supported but isolated clade near the base of *Solanum*.

Non-molecular characters that may distinguish this clade include herbaceous habit and usually pinnately dissected and rather thick leaves, sometimes with winged petioles and stems. Plants of *Solanum montanum* and *S. multifidum* grown in the University of Utah greenhouse had nearly rotate corollas and notably expanded stigmas. *Solanum montanum* is reported to bear tubers (Dunal, 1852; Macbride, 1962), but the *ndh*F results do not suggest a direct relationship between the Regmandra clade and the tuber-bearing members of the Potato clade.

3. Archaesolanum clade

ca. 8 spp., Australia, New Guinea,
New Zealand

Included taxa:

Solanum subg. *Archaesolanum* Marzell

Solanum sect. *Archaesolanum*
(Marzell) Danert*

This is a distinctive group with no obvious close relatives within *Solanum*. It is distinguished by its aneuploid chromosome number based on $n = 23$, a number unique in the genus. All species of this group occur in Australia and the South Pacific (New Guinea, Australia, Tasmania, New Zealand). Aside from its chromosome number, possible non-molecular synapomorphies of this clade include plurifoliate sympodial units, rotate corollas with abundant interpetalar tissue, loosely erect anthers on relatively long filaments, and fruits with abundant stone cell aggregates. The basal position of this clade may indicate a relatively old radiation in the South Pacific.

The Archaesolanum clade has been recognized as distinct by virtually all previous *Solanum* workers, including D’Arcy (1972, 1991), Bitter in Marzell (1927), Danert (1970), and Symon (1994). Olmstead and Palmer (1997) included *S. aviculare* in their analysis of *Solanum* using chloroplast restriction site data, and it formed a clade with 76% bootstrap support along with *S. ptychanthum*, *S. crispum*, *S. dulcamara*, and *S. jasminoides*. However, sampling within non-spiny *Solanum* taxa was sparse in their study, with 17 non-spiny representatives out of 36 total *Solanum* species. Bohs and Olmstead (2001) found that *S. aviculare* and *S. laciniatum* formed a well-supported basal clade in *Solanum* in analyses using nuclear ITS sequence data as well as ITS combined with *ndh*F data. It seems safe to say that the Archaesolanum clade represents an isolated group whose closest relatives have not yet been identified.

4. Normania clade

3 spp., Macaronesia, Spain, NW Africa

Included taxa:

Solanum sect. *Normania* (Lowe) Bitter
[genus *Normania* Lowe]*
genus *Triguera* Cav.*

This clade includes two enigmatic groups endemic to Macaronesia and adjacent areas of Spain and northwestern Africa. Although these taxa have been recognized as the segregate genera *Normania* and *Triguera*, molecular data indicate that both are nested within *Solanum* and the three species of both genera have been transferred to *Solanum* (Bohs & Olmstead, 2001). Francisco-Ortega et al. (1993) made a thorough morphological analysis of *Normania* and *Triguera* and concluded that they were closely related.

Numerous non-molecular characters unite the species of the Normania clade, including herbaceous or weakly woody habit, foliaceous and accrescent calyces, zygomorphic corollas, subequal to very unequal stamens, anther dehiscence by both apical pores and longitudinal slits, anthers with horned projections, fruits dry or with sparse pulp, seeds large and few per fruit with the seed coat cell walls radially expanded, and pollen grains with colpi joined at the poles. Affinities of the Normania clade within *Solanum* are presently obscure. In combined analyses of *ndh*F and ITS data this clade forms a group with members of the Potato and Morelloid/Dulcamaroid clade (Bohs & Olmstead, 2001), but this placement is poorly supported, with a bootstrap value of 17%. As with the Archaesolanum clade, the Normania clade appears to form an isolated group within *Solanum* without obvious close relatives.

5. African non-spiny clade

ca. 7 spp., Africa

Included taxa:

- *Solanum* subg. *Lyciosolanum* Bitter*
- *Solanum* subg. *Solanum* pro parte
  - *Solanum* sect. *Afrosolanum* Bitter*
  - *Solanum* sect. *Quadrangulare* Bitter*
  - *Solanum* sect. *Benderianum* Bitter

D'Arcy (1972, 1991) recognized *Solanum* subg. *Lyciosolanum* as monotypic, with *S. aggregatum* as its sole member, but the *ndh*F data indicate that probably this group should be expanded to include members of *Solanum* sects. *Afrosolanum*, *Quadrangulare*, and perhaps *Benderianum*, all placed by D'Arcy (1972, 1991) in *Solanum* subg. *Solanum*. This clade forms an isolated group within *Solanum*. It is poorly known taxonomically, but possible non-molecular synapomorphies may include shrubby or climbing habit, unbranched or dendritically branched hairs, and purple or white stellate corollas. This group needs better molecular sampling and morphological characterization.

No DNA samples are available from representatives of *Solanum* sects. *Lemurisolanum* Bitter and *Macronesiotes* Bitter, two non-spiny sections endemic to Madagascar. Their affinities may lie with the African non-spiny clade or with the Dulcamaroid clade.

6. Potato clade

ca. 200–300 spp., New World

Included taxa:

- *Solanum* subg. *Potatoe* (G. Don) D'Arcy pro parte
  - *Solanum* sect. *Petota* Dumort.*
  - *Solanum* sect. *Anarrhichomenum* Bitter*
  - *Solanum* sect. *Basarthrum* (Bitter) Bitter*
  - *Solanum* sect. *Lycopersicon* (Mill.) Wettst.*
  - *Solanum* sect. *Neolycopersicon* Correll
  - *Solanum* sect. *Juglandifolium* (Rydb.) A. Child*
  - *Solanum* sect. *Etuberosum* (Bukasov & Kamaraz) A. Child*
  - *Solanum* sect. *Articulatum* (Correll) A. Child
  - *Solanum* sect. *Taeniotrichum* A. Child
- *Solanum* subg. *Bassovia* (Aubl.) Bitter pro parte
  - *Solanum* sect. *Herpystichum* Bitter*
  - *Solanum* sect. *Pteroidea* Dunal*

This clade includes most of the groups of D'Arcy's subgenera *Potatoe* and *Bassovia*. Child's treatment of subgenus *Potatoe* (Child, 1990; Child & Lester, 2001) included these groups, but his concept also encompassed a number of disparate elements that are placed here in different clades, such as *Solanum* sect. *Normania* (here placed in the Normania clade), the dulcamaroid taxa *sensu* Child and Lester (2001; sects. *Dulcamara*, *Jasminosolanum*, and *Californisolanum*, here placed in the Dulcamaroid clade), and the "anomalously prickly" taxa *sensu* Child (1990; sects. *Aculeigerum*, *Nemorense*, and *Herposolanum*, here placed in the Wendlandii/Allophyllum and Leptostemonum clades). Nee's recent *Solanum* scheme (Nee, 1999) considered the taxa that here belong to the Potato clade to represent two distinct evolutionary lines. He included the potatoes and their relatives (sects. *Petota*, *Anarrhichomenum*, *Basarthrum*) in a large and morphologically diverse subgenus *Solanum*, along with other groups such as sections *Dulcamara*, *Solanum*, *Holophylla*, *Brevantherum*, *Regmandra*, and *Archaesolanum*. He also included members of section *Herpystichum* in this clade. As Nee (1999) noted, the type of section *Herpystichum* is not known with certainty and the group is not well circumscribed, but he listed *S. phaseoloides* and *S. evolvulifolium* as members of the section. These species are sampled in the *ndh*F analyses, and they both fall out in the Potato clade.

On the other hand, Nee (1999) maintained *Solanum* subg. *Bassovia*, amplifying it to include sections *Cyphomandropsis* and *Pachyphylla* of the Cyphomandra clade and section *Allophylla* of the Wendlandii/Allophyllum clade along with section *Pteroidea*, which was placed in subgenus *Bassovia* by previous workers such as Bitter (1921), Seithe (1962), Danert (1970), and D'Arcy (1972). Knapp and Helgason (1997) revised the species of section *Pteroidea*, but they were unsure of the higher-level relationships of the section.

The *ndh*F data indicate that section *Pteroidea* belongs to the Potato clade, and that the sampled representatives of the subgenera *Potatoe* and *Bassovia sensu* D'Arcy (1972) each form monophyletic clades. Non-molecular synapomorphies that may unite both of these groups include herbaceous to weakly woody and often scandent habit, exclusively unbranched hairs, presence of rhizomes or tubers in many taxa, presence of compound leaves in most species, and lack of stone cell aggregates in the fruits. The presence of solanidine/tomatidine alkaloids may be the most consistent synapomorphy that defines the subgenus *Potatoe*. Whether members of the subgenus *Bassovia* possess these types of alkaloids is unknown.

Child (1990) placed *Solanum evolvulifolium* in section *Anarrhichomenum*, whereas Nee (1999) placed this species in section *Herpystichum*. The *ndh*F data show that *S. evolvulifolium* is more closely related to *S. phaseoloides* (sect. *Herpystichum*) than to *S. appendiculatum* (sect. *Anarrhichomenum*).

The placement of this monotypic *Solanum* sect. *Rhynchantherum* Bitter has been debated. Dunal (1852), D'Arcy (1972, 1991), and Hunziker (2001) assigned it to subgenus *Potatoe*, Bitter (1913a) proposed an affinity with *S. reptans* of section *Herposolanum* (cf. *S. hoehnei* in the Leptostemonum clade), and Miers (1855) and Child (1984b; Child & Lester, 2001) placed it in the genus *Cyphomandra* (Cyphomandra clade). Although no DNA data are available, its pinnately compound leaves and anther structure (described in Bohs, 1994) argue for placement in the Potato clade.

7. Morelloid/Dulcamaroid clade

This group comprises two subclades, which will be discussed separately. Bootstrap support for the association of the two groups is strong (94% of bootstrap replicates) in the *ndh*F data set, but additional molecular data from other genes are needed to ascertain whether this group should be better recognized as two separate clades. For instance, ITS data from a small subset of the taxa considered here provided weak support (19% of bootstrap replicates) for the association of the morelloid and dulcamaroid subgroups (Bohs & Olmstead, 2001).

7a. Morelloid clade

ca. 75 spp., worldwide

Included taxa:

- *Solanum* subg. *Solanum* pro parte
  - *Solanum* sect. *Solanum**
  - *Solanum* sect. *Campanulisolanum* Bitter*
  - *Solanum* sect. *Parasolanum* A. Child*
  - *Solanum* sect. *Episarcophyllum* Bitter*
  - *Solanum* sect. *Chamaesarachidium* Bitter

This clade includes the core of *Solanum* species often known as the morelloid taxa. The four sections exclusive of section *Parasolanum* are morphologically homogeneous, and sectional distinctions are not clear-cut. Three members of *Solanum* sect. *Parasolanum* (*S. tripartitum*, *S. palitans, S. triflorum*) were sampled in the *ndh*F analyses, and all are included in the morelloid clade. However, these three taxa do not fall out together, indicating that section *Parasolanum* as circumscribed by Child (1984a) may not be a monophyletic group. In the *ndh*F analyses, *S. tripartitum* and *S. palitans* form a strongly supported clade, which, in turn, is strongly associated with the rest of the Morelloid clade (95% bootstrap support). However, these two species form a separate group distinct from the rest of the Morelloid clade in trees based on ITS sequences (Bohs & Olmstead, 2001). More extensive ITS sampling along with molecular data from additional genes may enhance the circumscription and placement of section *Parasolanum*.

Some non-molecular characters that may serve to unite this clade include herbaceous or weakly woody habit, 2- to 3-foliate sympodial units, pubescent filaments and styles in many taxa, and small stone cell aggregates in the fruits.

7b. Dulcamaroid clade

ca. 40 spp., worldwide

Included taxa:

- *Solanum* subg. *Potatoe* (G. Don) D'Arcy pro parte
    - *Solanum* sect. *Dulcamara* Dumort.*
    - *Solanum* sect. *Jasminosolanum* Seithe*
    - *Solanum* sect. *Californisolanum* A. Child*
- *Solanum* subg. *Solanum* pro parte
    - *Solanum* sect. *Lysiphellos* (Bitter) Seithe
- *Solanum* subg. *Minon* Raf. pro parte
    - *Solanum* sect. *Holophylla* Walp. pro parte*

This clade consists of elements from three of D'Arcy's subgenera. Sectional limits are not well defined, and the majority of groups included here are in need of critical taxonomic revision and nomenclatural clarification. The *ndh*F results indicate that *Solanum* sect. *Holophylla* is not monophyletic as traditionally defined. Part of *Solanum* sect. *Holophylla* that includes the species *S. aligerum*, *S. pubigerum*, and members of the *S. nitidum* group [Knapp, 1989; equivalent to *S.* subsect. *Nitidum* A. Child (Child, 1998)] belongs to the Dulcamaroid clade. At least part of the remainder of *Solanum* sect. *Holophylla*, represented in the *ndh*F trees by *S. argentinum*, belongs to the Geminata clade. Morphological synapomorphies of the Dulcamaroid clade may include vining habit in many taxa, the presence of unbranched, dendritic, or echinoid hairs, 3- to many-foliate sympodial units, and fruits lacking stone cell aggregates.

The following clades form a large group in *Solanum* with 98% bootstrap support (Fig. 1). Although the majority of species in this group belong to the spiny *Solanum* subg. *Leptostemonum* (the Leptostemonum clade), four other predominantly non-spiny clades are represented here. This group is morphologically heterogeneous and has not been recognized formally at any rank.

8. Wendlandii/Allophyllum clade

ca. 10 spp., New World

Included taxa:

- *Solanum* sect. *Allophyllum* (Child) Bohs*
- *Solanum* subg. *Leptostemonum* pro parte
    - *Solanum* sect. *Aculeigerum* Seithe*

This clade is perhaps the most unusual and surprising in all of *Solanum*. Thus far it consists of two groups whose relationships to other *Solanum* taxa have been debated. Species of *Solanum* sect. *Allophyllum* were previously placed in the genus *Cyphomandra* (D'Arcy, 1973; Child, 1984b; Bohs, 1988), but Bohs (1989) showed that they did not have the characters of the Cyphomandra clade. The subgeneric placement of *Solanum* sect. *Allophyllum*, however, has been obscure (Bohs, 1990). *Solanum* sect. *Aculeigerum* has usually been placed in subgenus *Leptostemonum* because the plants bear spines (D'Arcy, 1972, 1991; Whalen, 1984). However, they lack stellate hairs, a hallmark of the subgenus, so some workers have placed this section in with the non-spiny species of *Solanum* in either subgenus *Solanum* (Seithe, 1962) or *Potatoe* (Child, 1990; Child & Lester, 2001). Molecular data of Bohs and Olmstead (1997, 1999, 2001) showed that *Solanum* sect. *Aculeigerum* probably does not belong in the spiny *Solanum* subg. *Leptostemonum*, but is instead allied to a spineless group, section *Allophyllum*. The *ndh*F analyses presented here continue to support that placement. Species of *Solanum* sections *Allophyllum* and *Aculeigerum* are morphologically distinctive, but both groups have narrow, tapered anthers that dehisce by small terminal pores, exclusively unbranched hairs, and frequently have pinnately lobed leaves.

9. *Cyphomandra* clade

ca. 50 spp., New World

Included taxa:

Solanum sect. *Pachyphylla* (Dunal) *Dunal* [genus *Cyphomandra* Sendtn.]*

Solanum sect. *Cyphomandropsis* Bitter*

Solanum sect. *Glaucophyllum* A. Child*

The association of these three sections and their relationship to *Solanum* have been controversial. From 1845 to 1995, *Cyphomandra* was recognized as a separate genus (Sendtner, 1845; Bohs, 1994, and references therein). However, molecular data establish that it is nested within *Solanum*, and all species of *Cyphomandra* were transferred to *Solanum* in 1995 (Bohs, 1995). *Solanum* sect. *Cyphomandropsis* was considered to be part of *Cyphomandra* by some workers (D'Arcy, 1972; Child, 1984b; Child & Lester, 2001), whereas others maintained this group in *Solanum* (Bitter, 1913b; Seithe, 1962; Gilli, 1970; Danert, 1970; Morton, 1976). Within *Solanum*, its subgeneric placement has been debated, with Seithe (1962) placing it in subgenus *Solanum* and Smith and Downs (1966) and Morton (1976) placing it in subgenus *Leptostemonum*. Most authors have considered *S. glaucophyllum* to belong to *Solanum* sect. *Cyphomandropsis*, but Child (1986) removed it to its own monotypic section and placed it in subgenus *Solanum*. Hunziker (2001) disagreed with this view on morphological grounds and placed it within *Solanum* subg. *Potatoe*. Morphological, cytological, and molecular studies have confirmed the close association of *Solanum* sections *Pachyphylla*, *Cyphomandropsis*, and *Glaucophyllum* (Morton, 1976; Moscone, 1992; Bohs, 2001; Bohs & Olmstead, 2001), and molecular data indicate that they form a distinct clade within *Solanum* whose close relatives are unclear (Fig. 1).

Species of the Cyphomandra clade are woody shrubs or trees that often have enlarged or elaborated anther connectives or dorsal anther surfaces. The synapomorphy that unites this group is the presence of very large chromosomes, which have been found in all species of the clade investigated to date.

10. Geminata clade

ca. 140 spp., mainly New World

Included taxa:

Solanum subg. *Solanum* pro parte

Solanum sect. *Geminata* (G. Don) Walp.*

Solanum sect. *Delitescens* Hunz. & Barboza*

Solanum sect. *Diamonon* (Raf.) A. Child*

Solanum subg. *Minon* Raf. pro parte

- *Solanum* sect. *Holophylla* pro parte*
- *Solanum* sect. *Pseudocapsicum* (Moench) Bitter*

Although placed by D'Arcy (1972, 1991) in separate subgenera of *Solanum*, both morphological studies (Knapp, 2002) and the *ndh*F analyses confirm that section *Geminata* and section *Pseudocapsicum* are closely related. Both groups have mainly leaf-opposed inflorescences and often 1- to 2-foliate sympodial units. Yet other elements belong to the Geminata clade, such as *S. argentinum*, *S. delitescens*, and *S. havanense*. *Solanum argentinum* has been placed in section *Holophylla*, but this group is apparently polyphyletic, with at least part of the section belonging to the Dulcamaroid clade.

The systematic position of *S. delitescens* has been unclear. Knapp (2002) includes it in her treatment of *Solanum* sect. *Geminata*, but lists it under taxa of uncertain placement. Nee (1999) included it within the heterogeneous *Solanum* sect. *Holophylla* within subgenus *Solanum*. Hunziker and Barboza (in Hunziker, 2000) created the monotypic *Solanum* sect. *Delitescens* to accommodate this species and also placed it within subgenus *Solanum*. The *ndh*F data indicate that *Solanum* sections *Geminata*, *Pseudocapsicum*, and *Delitescens* are closely related to each other and are not allied with the morelloid species that make up the core of subgenus *Solanum*.

Likewise, the affinities of *Solanum havanense* have been uncertain. This species occurs in Cuba and Jamaica and, according to Knapp (2002), is allied to the Jamaican species *S. troyanum* Urb. Knapp (2002) excluded these two species from *Solanum* sect. *Geminata* and regarded them as an isolated lineage in *Solanum*, which she called the *S. havanense* species group (Knapp, 2002). Child (1998) created the monotypic *Solanum* sect. *Diamonon* to accommodate *S. havanense* and hypothesized that it may belong near section *Pseudocapsicum*. In the *ndh*F trees, *S. havanense* belongs to the *Geminata* clade along with members of *Solanum* sections *Geminata*, *Pseudocapsicum*, and *Delitescens*.

Characters that may unite the taxa of this clade include woody habit, unbranched to dendritically branched hairs, oblong anthers with large terminal pores, and fruits lacking stone cell aggregates.

11. Brevantherum clade

ca. 60 spp., New World

Included taxa:

Solanum subg. *Brevantherum* (Seithe) D'Arcy pro parte [*Solanum* subg. *Minon* pro parte in D'Arcy (1991)]

- *Solanum* sect. *Brevantherum* Seithe*
- *Solanum* sect. *Extensum* D'Arcy*
- *Solanum* sect. *Lepidotum* Seithe*
- *Solanum* sect. *Stellatigeminatum* A. Child*
- *Solanum* sect. *Cernuum* Carvalho & G. J. Sheph.

Solanum subg. *Solanum* pro parte

- *Solanum* sect. *Gonatotrichum* Bitter*

For the most part, this clade consists of a number of morphologically similar groups that often have stellate hairs or lepidote scales, oblong anthers with large terminal pores, and green, yellow, or purple fruits. D'Arcy (1991) used the subgeneric name *Minon* to refer to an analogous group in *Solanum*, which, however, also included elements such as sections *Holophylla* and *Pseudocapsicum* that are here referred to different clades. Since the type species of subgenus *Minon* is *S. pseudocapsicum*, which belongs to the Geminata clade, the appropriate name for the Brevantherum clade at subgeneric rank would be *Solanum* subg. *Brevantherum*.

The sections of *Solanum* subg. *Brevantherum* are not well demarcated. The three members of *Solanum* sect. *Brevantherum* (*S. abutiloides*, *S. mauritianum*, *S. rugosum*) sampled in the *ndh*F trees do not form a monophyletic group, but additional data and sampling are needed to resolve relationships in the Brevantherum clade. There are a number of species that fall outside the traditional limits of the established sections listed above. One example is *Solanum inelegans*, placed by Nee (1999) in the polymorphic and ill-defined *Solanum* sect. *Holophylla* and evidently a member of the Brevantherum clade according to the *ndh*F data.

The odd group out from a morphological perspective is *Solanum* sect. *Gonatotrichum* (*S. adscendens*, *S. turneroides*, *S. deflexum*). Its placement here is surprising, because *Solanum* sect. *Gonatotrichum* has few of the characters listed above for the Brevantherum clade and has been thought to be more closely related to the Morelloid clade (D'Arcy, 1972, 1991; Nee, 1999; Child & Lester, 2001) or to *Solanum* sect. *Pseudocapsicum* of the Geminata clade (Hunziker, 2001). Molecular data indicate that *Solanum* sect. *Gonatotrichum* forms a distinct subclade within the Brevantherum clade (Fig. 1), but it clearly does not belong to the Morelloid clade. The names *S. adscendens* and *S. deflexum* may be synonymous (Nee, 1989, 1999; D'Arcy, 2001) but the two species exhibit a fair amount of sequence divergence in *ndh*F (1.0%) and are apparently allopatric (Bitter, 1912).

12. Leptostemonum clade

ca. 450 spp., worldwide

Includes all spiny sections and species groups except *Solanum* sect. *Aculeigerum* Seithe

Possibly includes *Solanum* sect. *Herposolanum* Bitter

Sampling to date includes at least 20 sections and 20 species groups *sensu* Whalen (1984)

This is the largest and most complex of the major clades of *Solanum* and encompasses the vast majority of species traditionally placed in *Solanum* subg. *Leptostemonum*. Data thus far indicate that all the species of *Solanum* that bear spines form a clade with the exception of section *Aculeigerum* mentioned above. Nearly all members of this group have stellate hairs as well as spines. The anthers are narrow and tapered with small terminal pores that do not enlarge into longitudinal slits. Much work is still needed to reveal the phylogenetic structure within the Leptostemonum clade and to interpret patterns of character evolution and biogeography within the group. A more detailed analysis of the Leptostemonum clade using *ndh*F and nuclear ITS sequence data is under way (L. Bohs, unpublished data) and will be summarized in a later publication.

The *ndh*F data indicate members of *Solanum* sections *Nemorense* (*S. nemorense*) and *Herposolanum* (*S. hoehnei*) may represent the basalmost branches in the Leptostemonum clade, but the bootstrap support for this grouping is low (51%). These taxa are similar to *Solanum* sect. *Aculeigerum* in that they have spines but lack stellate hairs. The placement of *Solanum* sect. *Herposolanum* has been particularly problematic; D'Arcy (1972, 1991) put it into *Solanum* subg. *Bassovia*, whereas Child (1983) suggested a relationship with *Solanum* sect. *Aculeigerum* (the Wendlandii/Allophyllum clade above) and provisionally placed it in *Solanum* subg. *Potatoe* (Child, 1990; Child & Lester, 2001). Whalen (1984) merged *Solanum* sections *Herposolanum* and *Nemorense* into his *S. nemorense* species group, which he considered to belong to *Solanum* subg. *Leptostemonum*. Nee (1999) included *Solanum* sect. *Aculeigerum* in section *Herposolanum* and regarded both as members of subgenus *Leptostemonum*. The *ndh*F data do not fully resolve these questions, but *Solanum* sections *Herposolanum* and *Nemorense* apparently do not belong to the Potato clade and are not closely related to section *Aculeigerum*.

Solanum sect. *Acanthophora* (*S. capsicoides*, *S. mammosum*) also appears to be relatively basal in the Leptostemonum clade. This group often has unbranched or weakly stellate hairs in addition to spines. These have been interpreted as being reduced stellate hairs (Nee, 1979), but a thorough examination of the ontogeny of hairs in this clade should be undertaken with a phylogenetic perspective to determine if these simple hairs represent an ancestral rather than derived state in the Leptostemonum group.

GENERAL RECOMMENDATION

This is not the last word on phylogenetic structure or evolutionary relationships in *Solanum*. The major clades identified here, although well supported from *ndh*F data, need to be corroborated by data from other genes. Additional sampling, especially from morphologically unusual, underrepresented, and/or putatively isolated groups, is needed to test the distinctiveness of the major *ndh*F clades and to ascertain the phylogenetic position of enigmatic taxa. For instance, no molecular data are available for the two species placed in *Solanum* sect. *Solanocharis* (Bitter) A. Child. The two species may not be closely related (M. Nee, pers. comm.), and they may not belong to *Solanum*. The type of the section is *S. albescens* (Britton) Hunz., which apparently has longitudinal anther dehiscence and has been regarded by some as belonging to the genera *Solanocharis*, *Poecilochroma*, or *Saracha* (Rusby, 1896; Bitter, 1918; M. Nee, pers. comm.). Molecular data will certainly aid in the interpretation of this puzzling group.

Morphological and biochemical characters also should be examined, especially in the light of molecular findings, in order to identify nonmolecular synapomorphies that support the *ndh*F clades. Taxonomic studies at lower levels to demarcate species limits are desperately needed for many subgeneric groups. Many nomenclatural issues also need careful clarification.

In light of these uncertainties, new formal taxonomic designations for infrageneric categories in *Solanum* are strongly discouraged without more extensive data and sampling. Progress will not be facilitated by the creation of yet more formal names that must be sifted through by all subsequent workers in the group. Informal names for species groups or clades (e.g., Whalen, 1984; Knapp, 1989, 2000, 2002; Bohs, 1994, 2001) are encouraged until enough data have accumulated to positively demarcate and define distinct evolutionary units within *Solanum*.

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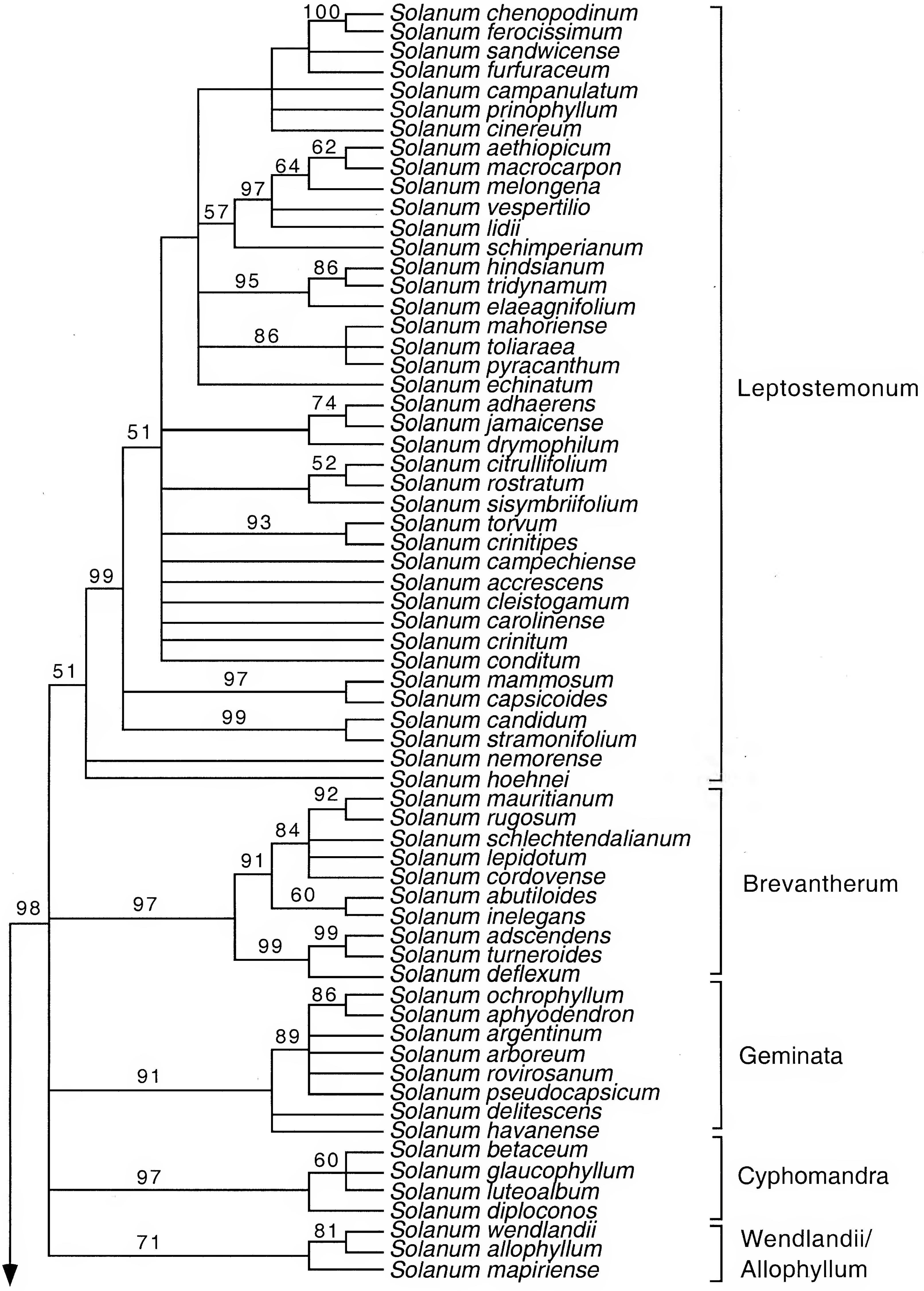
100
Solanum chenopodinum
Solanum ferocissimum
Solanum sandwicense
Solanum furfuraceum
Solanum campanulatum
Solanum prinophyllum
Solanum cinereum
62
Solanum aethiopicum
64
Solanum macrocarpon
97
Solanum melongena
57
Solanum vespertilio
Solanum lidii
Solanum schimperianum
86
Solanum hindsianum
95
Solanum tridynamum
Solanum elaeagnifolium
86
Solanum mahoriense
Solanum toliaraea
Solanum pyracanthum
Solanum echinatum
74
Solanum adhaerens
Solanum jamaicense
51
Solanum drymophilum
52
Solanum citrullifolium
Solanum rostratum
Solanum sisymbriifolium
93
Solanum torvum
Solanum crinitipes
Solanum campechiense
99
Solanum accrescens
Solanum cleistogamum
Solanum carolinense
Solanum crinitum
Solanum conditum
51
97
Solanum mammosum
Solanum capsicoides
99
Solanum candidum
Solanum stramonifolium
Solanum nemorense
Solanum hoehnei
92
Solanum mauritianum
Solanum rugosum
84
Solanum schlechtendalianum
91
Solanum lepidotum
Solanum cordovense
60
Solanum abutiloides
98
97
Solanum inelegans
99
Solanum adscendens
99
Solanum turneroides
Solanum deflexum
86
Solanum ochrophyllum
Solanum aphyodendron
89
Solanum argentinum
Solanum arboreum
91
Solanum rovirosanum
Solanum pseudocapsicum
Solanum delitescens
Solanum havanense
Solanum betaceum
60
97
Solanum glaucophyllum
Solanum luteoalbum
Solanum diploconos
81
Solanum wendlandii
71
Solanum allophyllum
Solanum mapiriense
Leptostemonum
Brevantherum
Geminata
Cyphomandra
Wendlandii/
Allophyllum

Figure 1. Strict consensus of 18,200 trees of 1053 steps from parsimony analysis of *ndh*F data. Numbers above branches are bootstrap values (500 replicates). Major clades in *Solanum* discussed in the text are labeled.

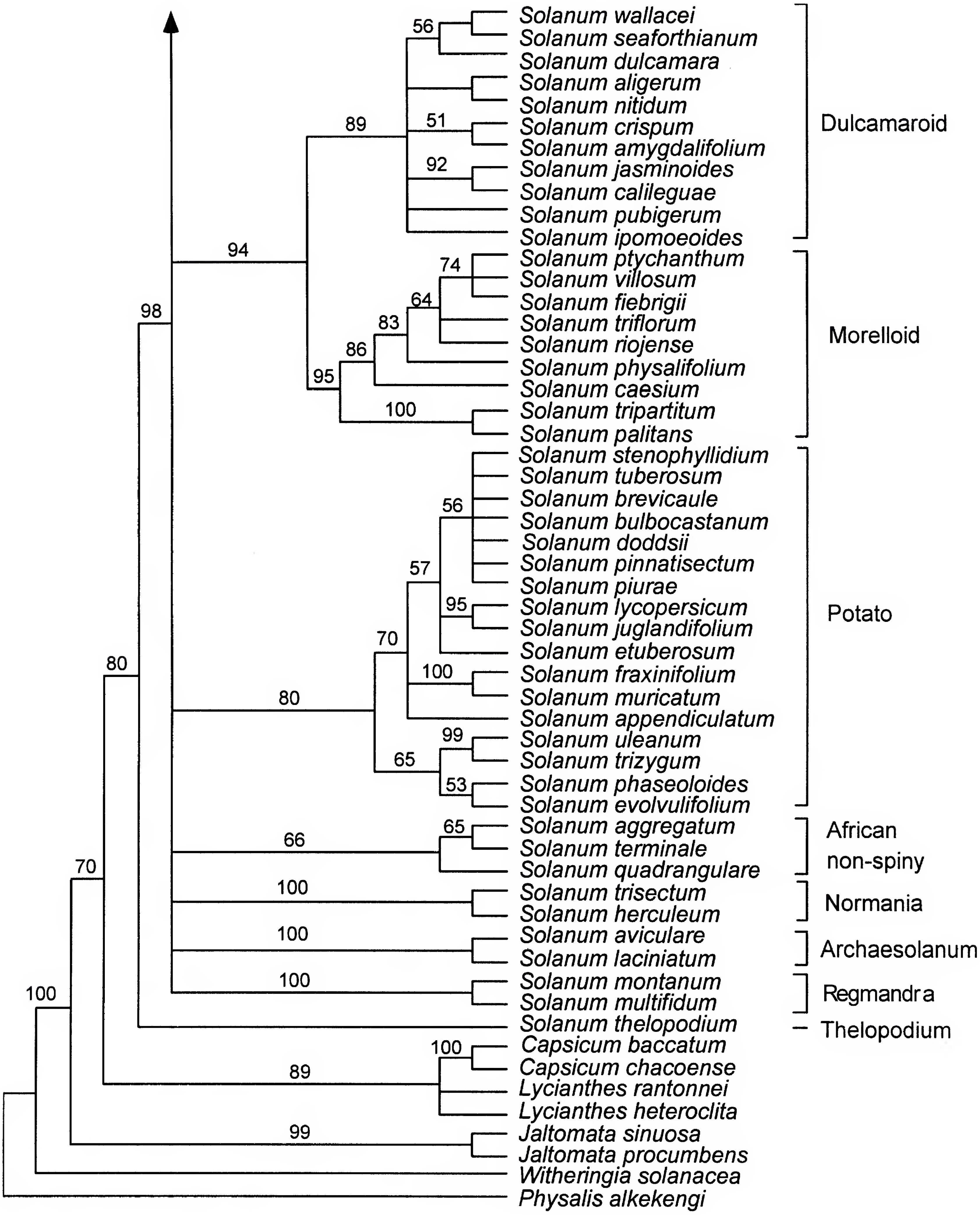
Solanum wallacei
Solanum seaforthianum
Solanum dulcamara
Solanum aligerum
Solanum nitidum
Solanum crispum
Solanum amygdalifolium
Solanum jasminoides
Solanum calileguae
Solanum pubigerum
Solanum ipomoeoides
Solanum ptychanthum
Solanum villosum
Solanum fiebrigii
Solanum triflorum
Solanum riojense
Solanum physalifolium
Solanum caesium
Solanum tripartitum
Solanum palitans
Solanum stenophyllidium
Solanum tuberosum
Solanum brevicaule
Solanum bulbocastanum
Solanum doddsii
Solanum pinnatisectum
Solanum piurae
Solanum lycopersicum
Solanum juglandifolium
Solanum etuberosum
Solanum fraxinifolium
Solanum muricatum
Solanum appendiculatum
Solanum uleanum
Solanum trizygum
Solanum phaseoloides
Solanum evolvulifolium
Solanum aggregatum
Solanum terminale
Solanum quadrangulare
Solanum trisectum
Solanum herculeum
Solanum aviculare
Solanum laciniatum
Solanum montanum
Solanum multifidum
Solanum thelopodium
Capsicum baccatum
Capsicum chacoense
Lycianthes rantonnei
Lycianthes heteroclita
Jaltomata sinuosa
Jaltomata procumbens
Witheringia solanacea
Physalis alkekengi
Dulcamaroid
Morelloid
Potato
African non-spiny
Normania
Archaesolanum
Regmandra
Thelopodium
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Figure 1 continued.

4

REVISION OF *SOLANUM FIEBRIGII* AND *SOLANUM SINUATIEXCISUM*, AND THEIR INCLUSION IN SECTION *CAMPANULISOLANUM*

Gloria E. Barboza and Armando T. Hunziker[†]

ABSTRACT. Two species of *Solanum* L. (*S. fiebrigii* Bitter and *S. sinuatiexcisum* Bitter) are included in section *Campanulisolanum* Bitter. Both of them had previously been allocated to section *Solanum*, from which they are now removed on the basis of some new relevant floral characters (pedicel, androecium, gynoecium). The species are described and illustrated, and a map of their geographic distribution is also presented.

Key words: *Solanum*, *Solanum* sect. *Campanulisolanum,* South America.

Since Bitter (1912) established section *Campanulisolanum* Bitter, its validity has been questioned by different authors. The section has been defined by its peculiar corolla shape and color, though Bitter himself mentioned its close affinity with section *Solanum* (sub nom. *Morellae*). Later, Seithe (1962), Danert (1970), and D'Arcy (1972) followed this criterion in their respective infrageneric systems, but they did not add any other novel character to differentiate the members of both sections of *Solanum* L. In the diverse and precise contributions by Edmonds (1972, 1977, 1978, 1979) on the taxonomy of the South American species of section *Solanum*, the British botanist provisionally included in this section the species that Bitter had assigned to section *Campanulisolanum* (i.e., *S. fiebrigii* Bitter and *S. sinuatiexcisum* Bitter). More recently, Child (1998) and then Nee (1999) agreed to subordinate section *Campanulisolanum* at a subsectional level under section *Solanum*.

Over ten years ago, we reported a comparative analysis of the androecium in some *Solanum* species, together with its taxonomical and evolutionary importance (Barboza & Hunziker, 1991). There, we included the morphology and histology of anthers of *Solanum fiebrigii* and pointed out the possible use of the anther features for the infrageneric classification of the large genus *Solanum*.

With the intention of modernizing the good treatments of Morton (1976) and Edmonds (1972, 1977, 1978) in relation to the South American section *Solanum*, we have again revised the species allocated to section *Campanulisolanum*. As a result, we found consistent and well-defined flower characters that justify the formal validity of this small section.

MATERIALS AND METHODS

This revision is based on the examination of over 110 herbarium specimens and on pickled material preserved in FAA (formalin-acetic acid-ethanol). Trichomes were analyzed from epidermal peels of the different plant organs. Preparation of herbarium material required boiling in water for a few minutes and the addition of two or three drops of soap in order to facilitate the hydration. After rinsing in at least two changes of water, the material was stained with safranin and mounted temporarily in glycerine prior to examination. The methodology used to analyze the anther of *Solanum* species is the same as in Barboza and Hunziker (1991); the anthers of *S. sinuatiexcisum* and *S. americanum* were stained with blue cresyl. Pictures were taken with an Axiophot microscope.

Pollen material was obtained from anthers of herbarium specimens or plants in the field fixed in FAA. Samples for light microscope study were acetolyzed according to the method of Erdtman (1960), and mounted in glycerine jelly. For scanning electron microscopy (SEM), non-acetolyzed grains were dehydrated in an alcohol series, pipetted on to an SEM stub in a few drops of 96% alcohol, and allowed to dry. Samples were coated with gold/palladium and examined using a JEOL JSM 35CF microscope (INSIBIO-CONICET). Measurements given are based on 20 pollen grains of at least five collections from each taxon. Descriptive terminology follows Punt et al. (1994). Seeds were soaked in water and sterilized in a 5–10% commercial bleaching agent. The seeds were then washed twice, air dried, and coated with gold/palladium for SEM.

CHARACTERS OF TAXONOMICAL IMPORTANCE AND TAXONOMIC RELATIONSHIPS

Recently, Hunziker (2001) proposed seven sections within subgenus *Solanum* and provided a tentative key and descriptions to circumscribe each one. Undoubtedly, the closest affinity of section *Campanulisolanum* is with section *Solanum.* Both taxa have many common characters including trichome morphology, the shape and division of leaves, the type and position of the inflorescence, the number of flowers per inflorescence, the calyx features, the pollen morphology, and the fruit and seed morphology. The major differences are in the plant habit, pedicels, corolla, androecium, and gynoecium (style). We will discuss the common and the differential characters as follows:

HABIT

Members of *Solanum* sect. *Campanulisolanum* are shrubs or much-branched robust herbs, to as much as 2.5 m tall, viscid, and slightly ill-smelling; the stems are hollow and striate, with the basal branches woody and the upper branchlets slender, mostly erect, and herbaceous. In *Solanum* sect. *Solanum*, the habit is mostly herbaceous and occasionally shrubby; furthermore, within the glandular-viscid species of this section, plant heights scarcely reach 1 m.

INDUMENTUM

Solanum species of section *Campanulisolanum* are densely viscid-pubescent, bearing exclusively simple and uniseriate glandular and non-glandular trichomes. There are two kinds of glandular trichomes, the most abundant ones being long, flexuous, multicellular (stalk 5- to 8-celled, smooth or striate cuticle; head dark, elliptical, and single-celled). In the second variant, the glandular trichomes are very short (bicellular stalk, smooth cuticle; head globose, 5- to 6-celled). Long-stalked glandular trichomes vary in length, and are especially typical of stems, leaves, the peduncle, pedicels, and the calyx (Figs. 1F, 2G). Short-stalked trichomes are less frequent and appear above all on leaf nerves and calyx (Figs. 1I, 2A). The non-glandular trichomes are always multicellular (2- to 6-celled), and their ornamentation varies according to the organs: finely verrucate or striated on the vegetative organs (Fig. 2F) and the external surface of calyx and corolla; the stylar ones are striated but the filaments bear smooth simple trichomes (Fig. 2M). The epidermal trichome morphology in this section agrees with that described by Edmonds (1982) for *Solanum* sect. *Solanum*. However, Edmonds (1982: 166) pointed out that "the epidermal hair morphology can be of some taxonomic value in the differentiation of taxa belonging to *Solanum* sect. *Solanum*, when used in conjunction with other taxonomic characters." This is not the case for the two species of *Solanum* sect. *Campanulisolanum*. In fact, the different variants of glandular and non-glandular trichomes observed are present in both species.

LEAVES

The leaves are petiolate and simple, with the apex acuminate or very acuminate and the base truncate or attenuate. The leaf margin division is an important character for distinguishing the two species of *Solanum* sect. *Campanulisolanum*; it is serrulate in *S. fiebrigii* (Fig. 1B) and serrate or mostly dentate in *S. sinuatiexcisum* (Fig. 2C). Leaf texture is membranaceous. The leaf margin shape ranges from entire to variously serrate-dentate in the species of *Solanum* sect. *Solanum*, and it is not sufficiently distinct from that of *Solanum* sect. *Campanulisolanum* to be useful as a diagnostic character.

INFLORESCENCES

As in *Solanum* sect. *Solanum*, the position of the inflorescence is always extra-axillary, short or long pedunculate, either unbranched (umbelliform cyme, Fig. 2B, C) or bifurcate or up to five-forked (Fig. 1B, C). The peduncle (length from the stem to the point where the pedicels or branches arise) is erect and elongate. In *Solanum* sect. *Campanulisolanum*, the pedicels are articulate at the base, leaving noticeable scars on the rachis, in contrast to the non-articulate pedicels of *Solanum* sect. *Solanum*.

FLOWERS

The flowers in both *Solanum* sect. *Solanum* and section *Campanulisolanum* are actinomorphic and pentamerous, with the calyx lobes generally being unequal, shorter or longer than the tube (Figs. 1E, 2J). However, the corolla is campanulate; its lobes are reduced to five inconspicuous tips (Figs. 1E, 2D); it has a delicate fragrance and is entirely light purple or violet,

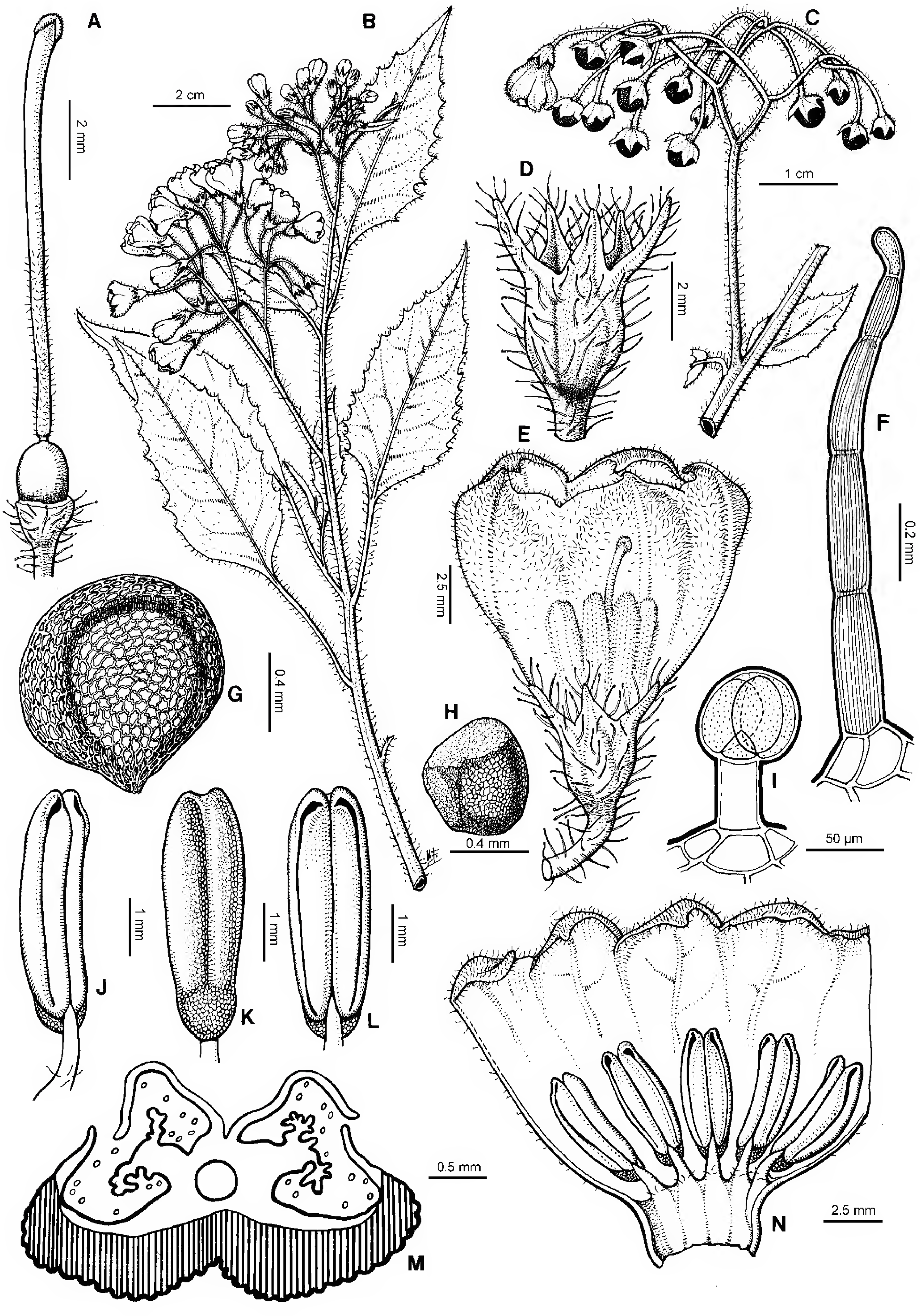
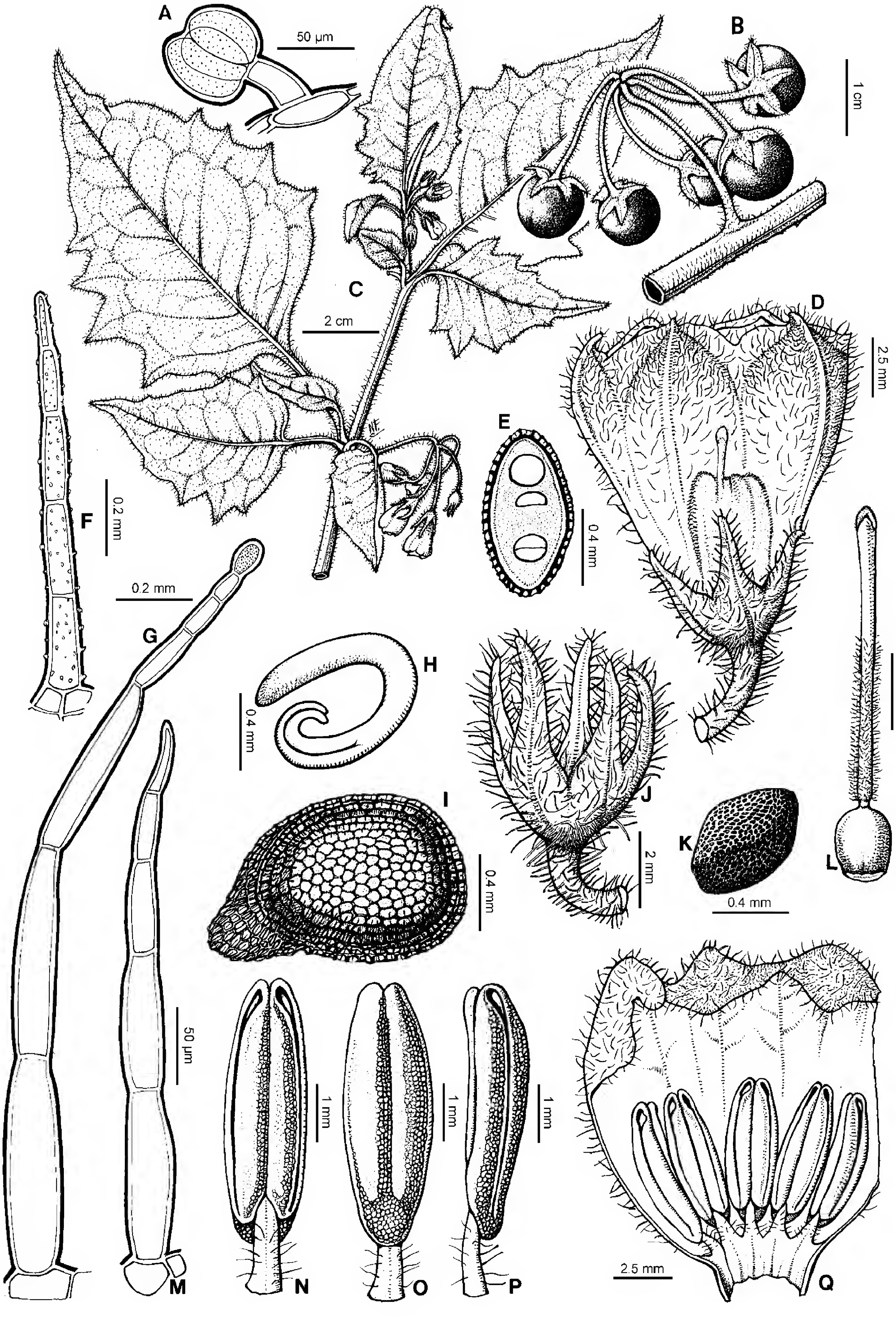

A
2 mm
B
2 cm
C
1 cm
D
2 mm
E
F
0.2 mm
2.5 mm
0.4 mm
G
H
0.4 mm
I
50 µm
1 mm
J
1 mm
K
1 mm
L
0.5 mm
M
2.5 mm
N

Figure 1. *Solanum fiebrigii.* —A. Gynoecium (note the articulation at its base). —B. Floriferous branch. —C. Section of a fructiferous branch. —D. Calyx. —E. Flower, lateral view. F, I. Glandular calyx trichomes. —F. One-celled head, striated stalk. —I. Multicellular head. —G. Immature seed. —H. Sclerosome. —J–L. Anther in lateral, dorsal, and ventral view, respectively (observe the papillate and prolonged dorsum of the anther). —M. Transverse section of the anther showing the thickness and glandular zone of the dorsal face (striped area). —N. Corolla opened to show the insertion of stamens. A, B, D–F, I–N based on *Hunziker 10093* (CORD); C, G, H based on *Ahumada et al. 8551* (CORD).


A
50 µm
B
1 cm
C
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D
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F
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G
H
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I
0.4 mm
J
2 mm
K
0.4 mm
L
2 mm
50 µm
M
1 mm
N
1 mm
O
1 mm
P
2.5 mm
Q

Figure 2. *Solanum sinuatiexcisum.* —A. Glandular leaf trichomes. —B. Section of a fructiferous branch. —C. Floriferous branch. —D. Flower, lateral view. —E. Transverse section of the seed. —F. Non-glandular verrucate leaf trichome. —G. Glandular calyx trichome. —H. Embryo. —I. Seed, lateral view. —J. Calyx. —K. Sclerosome. —L. Gynoecium (note the articulation at its base). —M. Non-glandular filament trichome. —N–P. Anther in ventral, dorsal, and lateral view, respectively (observe the prolonged dorsum of the anther). —Q. Corolla opened to show the insertion of stamens. A, C, D, F, G, J, L–Q based on *Solomon 13073* (CORD); B, E, H, I, K based on *Nee & Solomon 36671* (CORD).

sometimes with a dark purple or yellow ring at the base. This corolla shape is uncommon within the genus *Solanum*, and differs considerably from the well-defined stellate corollas with more or less deep lobes of the section *Solanum* species. In relation to the color, in section *Solanum* corollas are often immaculately white, or with an inner yellow basal star, though purple corollas can occur.

The filaments of the five fertile stamens are pubescent in their free sectors and shorter or longer than the portion fused to the corolla; the anthers are ellipsoidal and ventrifixed, dehiscing by a pore and a longitudinal slit; the thecae are free in the basal 1/10 part of their length and scarcely separated at the apex (Figs. 1N, 2Q). The most remarkable features of this whorl are the morphology and the histology of the dorsal face of the anthers. In fact, in the two *Solanum* species of section *Campanulisolanum*, the dorsum is characteristically prolonged beyond the length of the anther in a spur-like appendix (Figs. 1J–L, 2N–P) remaining free from the filament (Hunziker, 2001). Concerning the histology, in both the thick dorsal face, and in the appendix, the epidermis and the subjacent layers develop as a glandular structure. The cellular features of this structure have already been described in *S. fiebrigii* (Barboza & Hunziker, 1991), and the anthers of *S. sinuatiexcisum* have similar glandular tissue (Fig. 3B, E–G). On the contrary, in the species of *Solanum* sect. *Solanum*, the anther dorsum thickness is quite different since it is only 4- to 6-layered, non-glandular, and lacking the prolonged connectival appendix (pers. obs.), as is observed in *Solanum americanum* Mill. (Fig. 3A). *Solanum chenopodioides* Lam. (Fig. 3C, D) would be the only species within section *Solanum* with a proximal connectival appendix, but in this case it is non-glandular and hardly developed (Barboza & Hunziker, 1991).

The gynoecium in *Solanum* sect. *Campanulisolanum* measures ca. 8–12 mm long: the ovary is ovoid or subglobose, glabrous; the style is straight, slightly narrow and articulate at its base (vs. non-articulate in sect. *Solanum*), pubescent in the basal 1/4 or up to past its midpoint, extending 1–4 mm beyond anthers, sometimes exceeding the corolla length (Figs. 1A, 2L); and the stigma is always saddle-shaped.

POLLEN

The pollen morphology is very similar in both species (Fig. 4A–D). Pollen grains are small to medium-sized (polar axis: 16.5–28.2 μm), oblate spheroidal, outline in polar view (= amb) angular, sides of the outline convex, tricolporate; the colpi are distinct, long, and narrow, with more or less circular pores protruding from the center of each colpus; the aperture membrane is granular and the polar area small (polar area index: 0.12–0.20). The exine is 1.6–2 μm in thickness and moderately and uniformly microgranulate. The pollen grains of *Solanum* sect. *Campanulisolanum* are homogeneous and morphologically identical to those of section *Solanum* species (Edmonds, 1984).

FRUIT AND SEEDS

The berries are globose, 5–10 mm diam., and many-seeded (ca. 30–70 seeds); the calyx is slightly accrescent (Figs. 1C, 2B); the pericarp is thin and with up to 14 small sclerosomes; and the fruiting peduncle and pedicels are thin or stout, with the pedicels always deflexed. As in *Solanum* sect. *Solanum* (Edmonds, 1983), the mature seeds are globose or transovoidal in outline (Figs. 1G, 2I); the seed coat is honeycombed; the marginal cells are a little deeper than the central ones (Fig. 5A); and the epidermal cell walls are thickened and sinuate in outline (Fig. 5B). Strands of thickening, which appear as hair-like structures, arise from the lateral cell walls (Fig. 5B–D), these strands being covered by a thin outer tangential cell wall that is easily broken (Fig. 5C, D).

CHROMOSOMES

The basic chromosome number of the two species is $x = 12$. Both reports are mitotic counts: *S. fiebrigii*, $2n = 24$ (Edmonds & Chweya, 1997); *S. sinuatiexcisum*, $2n = 24$ (Edmonds & Chweya,

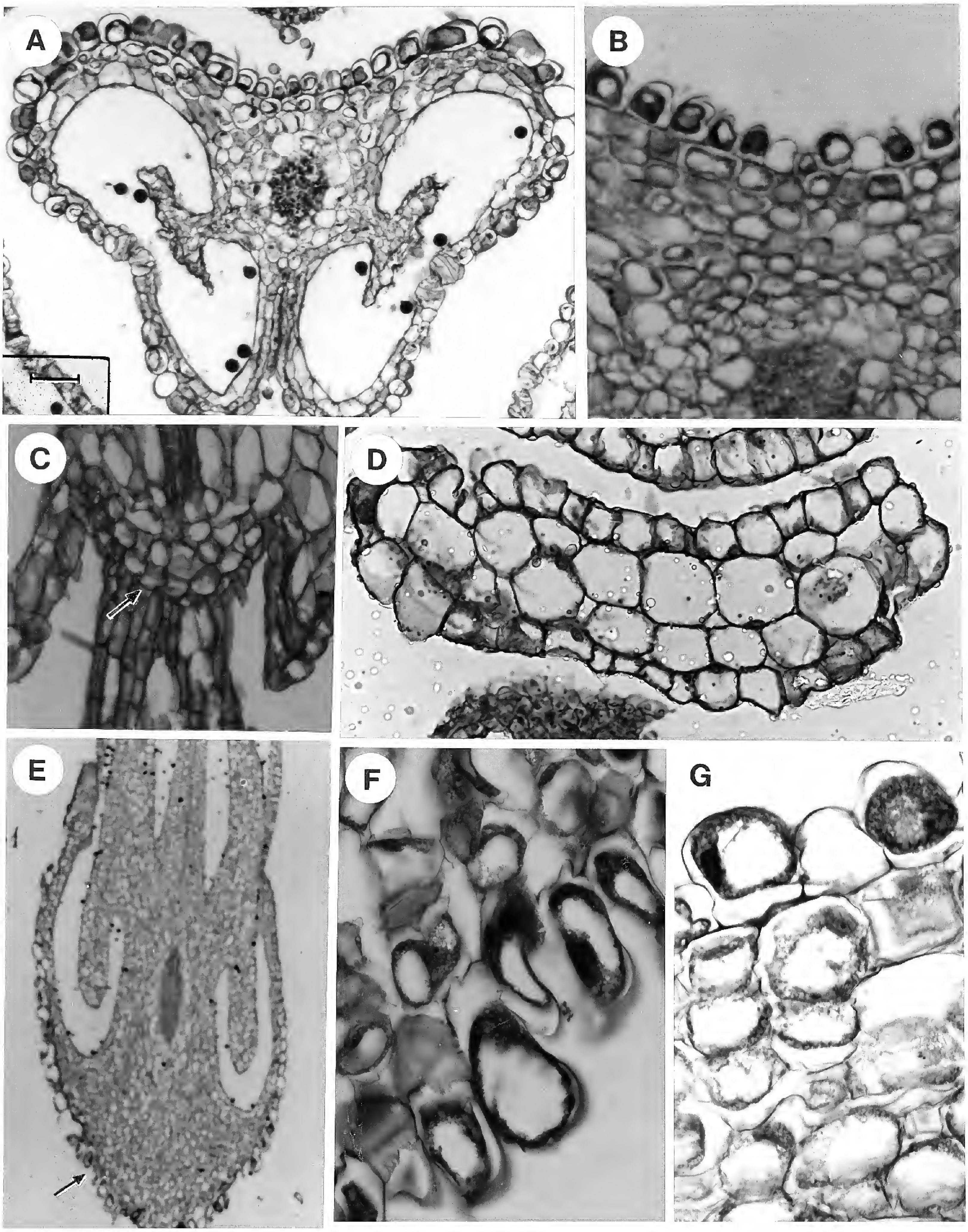

Figure 3. Anther anatomy in *Solanum.* —A. *Solanum americanum.* Cross section of an anther (observe the thin and non-glandular dorsum). B, E–G. *Solanum sinuatiexcisum.* —B. Sector of the thick dorsum of an anther, in cross section. —E. Proximal end of an anther showing the glandular appendix (arrow). —F, G. Details of the glandular tissue from the connectival appendix and the dorsum, respectively. C, D. *Solanum chenopodioides.* —C. Proximal end of a mature anther showing the inconspicuous connectival appendix (arrow). —D. Detail of the connectival appendix in cross section (note its non-glandular nature). Scale bar: A–C = 50 µm; D, F, G = 25 µm; E = 200 µm. A based on *Carrizo García s.n.* (CORD 585); B, E–G based on *Nee & Solomon 36671* (CORD); C, D based on *Dottori 137* (CORD).

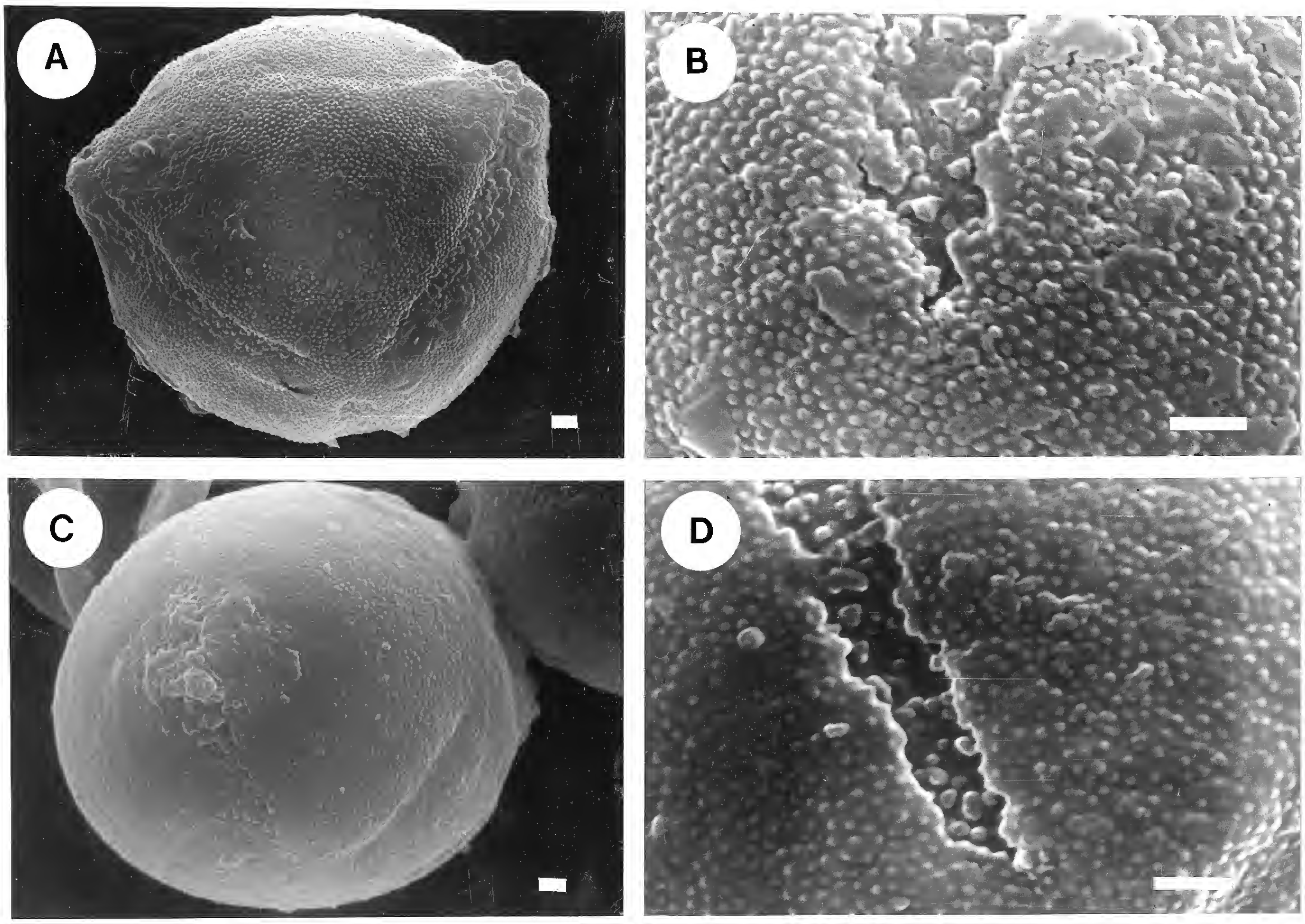

Figure 4. Pollen morphology of *Solanum* sect. *Campanulisolanum.* A, B. *Solanum fiebrigii.* —A. Polar view (observe the small polar area). —B. Aperture membrane with granule elements, and exine microgranulate. C, D. *Solanum sinuatiexcisum.* —C. Semi-equatorial view. —D. Aperture membrane with granule elements, and exine microgranulate. Scale bars: A–D = 1 µm. A, B based on *Hunziker 10093* (CORD); C, D based on *Solomon 13073* (CORD).

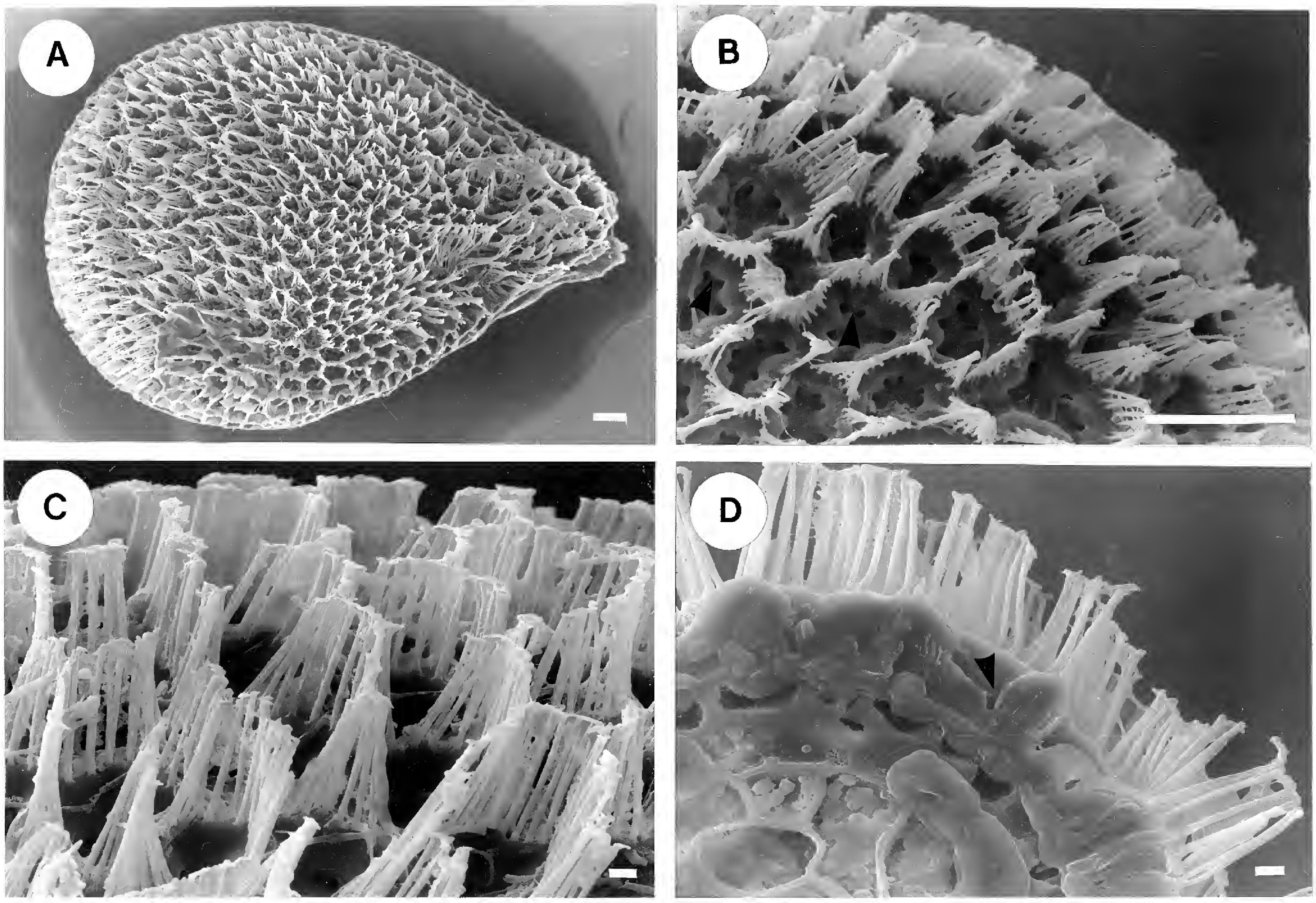

Figure 5. Seed coat structure of *Solanum sinuatiexcisum*. —A. Seed, lateral view. —B. Close-up of the seed coat showing the thickened cell walls (arrows). —C. Detail of outer epidermal cells showing strands of lateral thickening. —D. Transverse section of a seed (observe the inner tangential wall and basal part of the radial ones thickened, arrow). Scale bars: A, B = 100 µm; C, D = 10 µm. Based on *Nee & Solomon 36671* (CORD).

1997). The authors do not mention the specific origin of the material studied.

KEY TO *SOLANUM* SECT. *CAMPANULISOLANUM* AND SECT. *SOLANUM*

1a. Shrubs or robust herbs; pedicels articulate at the base; corolla campanulate, light purple or violet; anthers ventrifixed, with the dorsal glandular face thickened and prolonged in a spur beyond their basal end; style articulate basally...*Solanum* sect. *Campanulisolanum*

1b. Herbs, rarely shrubs; pedicels non-articulate at the base; corolla stellate, mostly white or rarely purple; anthers basifixed, with the dorsal non-glandular face thin and not prolonged in a spur beyond their basal end; style non-articulate basally...*Solanum* sect. *Solanum*

TAXONOMIC TREATMENT

Solanum sect. **Campanulisolanum** Bitter, Repert. Spec. Nov. Regni Veg. 11: 234. 1912. *Solanum* sect. *Solanum* subsect. *Campanulisolanum* (Bitter) Child, Feddes Repert. 109(5–6): 409. 1998. TYPE: *Solanum fiebrigii* Bitter (lectotype, designated by Seithe (1962: 287)).

Shrubs or robust herbs up to 2.5 m tall, viscid-pubescent; stems hollow, striate. Leaves petiolate, simple, the blade ovate or narrowly elliptical in outline, apex acuminate or very acuminate, base truncate or attenuate, margin serrulate, serrate, or dentate, (5–)7–16(–22.5) × (2.2)3–12 cm. Inflorescences extra-axillary, pedunculate, either unbranched (umbelliform cyme) or bifurcate or up to five-forked, multiflowered (4 to 52 flowers); pedicels articulate at the base; calyx lobes generally unequal, shorter or longer than the tube; corolla campanulate, lobes reduced to 5 inconspicuous tips, entirely light purple or violet or sometimes with a dark purple or yellow ring at the base, slightly fragrant, pubescent outside and glabrous inside, 10–15 mm long, 10–18 mm diam. at anthesis; filaments inserted near the corolla base, their free portion pubescent, shorter or longer than the sector fused to the corolla; anthers ellipsoidal, ventrifixed, poricidal-longitudinal, thecae free for the lower 1/10 of their length and scarcely separated at the apex, their dorsal face papillate, much thickened and basally prolonged beyond their total length in a spur-like appendix; pollen grains small- to medium-sized (polar axis = 16.5–28.2 μm), oblate spheroidal, tricolporate, microgranulate; gynoecium ca. 8–12 mm long, ovary ovoid or subglobose, glabrous, style straight, slightly narrow and articulate at its base, pubescent in the basal 1/4 or to past halfway up, stigma saddle-shaped. Fruits globose, 5–10 mm diam., many-seeded (ca. 30–70 seeds); calyx slightly accrescent; pericarp thin, with up to 14 small sclerosomes, fruiting peduncle and pedicels thin or stout, pedicels always deflexed. Seeds globose or trans-ovoidal in outline; the seed coat honeycombed; epidermal cell walls thickened and with strands of hair-like thickenings from the lateral cell walls. Embryo curved, cotyledons shorter than the rest of the embryo; endosperm abundant. $x = 12$.

Solanum sect. *Campanulisolanum* comprises only two species: *S. fiebrigii* and *S. sinuatiexcisum*. Recently, Child (1998) mentioned other species to be included in this section: *S. deltoideum* Rusby (Bolivia), *S. pallidum* Rusby (Bolivia), and *S. probolospermum* Bitter (Peru). This first species is a synonym of *S. sinuatiexcisum* (see below). *Solanum pallidum* is a species very distinct from section *Campanulisolanum* in its corolla (stellate shape) and the branched trichomes of its indumentum (Nee, pers. comm.). *Solanum probolospermum* does not appear to belong to section *Campanulisolanum* considering its rotate-stellate corolla, the terminal inflorescence, and the lack of the prolonged connective in the anthers.

The presence of *Solanum* sect. *Campanulisolanum* in Chile (Child, 1998) is doubtful; at least we have not found any specimen from this country in the herbaria studied.

KEY TO THE SPECIES OF *SOLANUM* SECT. *CAMPANULISOLANUM*

1a. Inflorescence forked or up to 4(to 5)-branched, 11- to 52-flowered; calyx 2.5–6 mm, lobes broadly triangular, 2–3.5 times shorter than the tube; style exceeding the anthers by 3–4 mm; berry small, ca. 5 mm diam., peduncle and pedicels thin; leaf margin serrulate...1. *S. fiebrigii*

1b. Inflorescence unbranched, umbellate, 4- to 7-flowered; calyx 5–12 mm, lobes narrowly triangular, 1.5 or 3 times longer than the tube; style exceeding the anthers by 2–2.3 mm; berry 7–10 mm diam., peduncle and pedicels stout; leaf margin serrate or dentate...2. *S. sinuatiexcisum*

1. **Solanum fiebrigii** Bitter, Repert. Spec. Nov. Regni Veg. 10: 556. 1912. TYPE: Bolivia [Argentina]. "Toldos prope Bermejo, juxta rivulum," 1800 m, 20 Dec. 1903 (fl, fr), *K. Fiebrig 2421* (lectotype, designated here, F not seen: photo + fragment; isotypes, G, NY: photo 2712!).

Solanum codonanthum Bitter, Repert. Spec. Nov. Regni Veg. 11: 235. 1912. TYPE: Argentina. "Tucumán, Siambon," Jan. 1874 (fl, fr), *P. G. Lorentz & G. Hieronymus 818* (lectotype, designated here, CORD!; isotype, US!).

Illustrations. A. L. Cabrera, Fl. Prov. Jujuy (Argentina) 8: 396, f. 171. 1983. Barboza & Hunziker, Kurtziana 21: 179, f. 1 I–L, N. 1991.

Herb or subshrub, 0.5–2 m high, viscid-pubescent; stems erect, edentate, longitudinally ridged, branches herbaceous, slightly ill-smelling, the crushed leaves odorless. Leaves solitary or sub-opposite near the apex, ovate or narrowly elliptical, the blade (5–)7–15(–16) × (2.2–)3–8.2 cm, the margins serrulate, with 7 to 13 (to 15) pairs of unequal and straight teeth directed upward, sinuses narrow, apex acuminate, base generally unequal and attenuate, both surfaces with long, abundant and patent glandular trichomes on the midvein and secondary veins, and scarce to abundant antrorse trichomes on the lamina; petiole 1.5–4.5 cm long. Inflorescence extra-axillary, forked or up to 4(to 5)-branched, 11- to 30(to 52)-flowered; peduncle 1.1–6.4(–7.3) cm long, pedicels 0.7–1.9 cm long; calyx (2.5)3.2–5.2(–6) mm long, lobes slightly unequal, triangular, 2 to 3.5 times shorter than the tube, (0.8)1.2–2.2 mm long; corolla 10–14 mm long, 13–18 mm diam. at anthesis, campanulate, light purple or violet, with a delicate fragrance, and few non-glandular trichomes on tips and margins; filaments inserted about 1.6 mm above the corolla base, their free portion pubescent, shorter or longer than the sector fused to the corolla (ca. 1–2 mm long); anthers ellipsoidal, 3.7–4 mm long, 1–1.2 mm wide, thickened and papillate dorsally and with a spur-like connectival prolongation; gynoecium ca. 9.8–12 mm long, ovary ovoidal, style pubescent only in its basal 1/4 or occasionally basal 1/2, 7.5–10 mm long, and 3–4 mm beyond anthers, sometimes exceeding the corolla length, stigma saddle-shaped, 0.4 mm long, 0.6 mm wide. Berry globose, small, ca. 5 mm diam, many-seeded (ca. 30), peduncle thin, 2.2–2.5 cm long, pedicels thin and deflexed, 1.4–1.6 cm long; pericarp with up to 14 small sclerosomes (0.5–0.7 mm diam.). Mature seeds not seen. Figures 1, 4A, B, 6.

Distribution and habitat. Known from Yungas Province (after Cabrera & Willink, 1980), inhabiting forests with rich and moist soil from southern Bolivia (Depts. Cochabamba, La Paz, Santa Cruz, and Tarija) to northern Argentina (Provs. Jujuy, Salta, Tucumán, and Catamarca), and rarely collected in southern Peru (Dept. Cuzco). It usually occurs at high elevations (1050–3700 m) and occasionally is found at lower altitudes (650–750 m).

Phenology. Flowering mainly from October to January; fruiting from November to April.

Uses. Ornamental herb or subshrub with attractive and fragrant blue or purple campanulate flowers (*in sched. Hunziker 10093, Lillo 2947, Nee 30342*).

Additional specimens studied. PERU. **Cuzco:** en Av. Los Incas y Perayoc, 25 May 1988, *P. Núñez & Ortega 9158* (MO, NY). BOLIVIA. Locality not indicated, 1847, *T. Bridges s.n.*, p.p. (BM, K). **Cochabamba:** Quebrada de Pocona, 12 Dec. 1928, *J. Steinbach 8707* (BM, G, K, NY, S, U); Valle de Cochabamba, 27 Dec. 1928, *J. Steinbach 8803*

(BM, G, K, NY, S); Cercado de Cochabamba, falderío Serranía Tunari, 24 Apr. 1966, *R. F. Steinbach 121* (NY, S); Tunari, Apr. 1963, *M. Cárdenas 6087* (K); Vila Vila, pumping station on the pipe-line, terminus of the rail Cochabamba to Santa Cruz, 17 Dec. 1949, *W. M. Brooke 5851* (BM, NY, U); Liriuni, 1 Oct. 1947, *R. Scolnik & Luti 598* (CORD, K, NY); Cervecería Taquiña, roadside, 6 Apr. 1963, *D. Ugent 4623* (K); Toralapa, Jan. 1946, *M. Cárdenas 3571* (US); 12 km N of Cochabamba, canyon above Taquina, 1 Nov. 1942, *M. Cárdenas & Cuteer 7417* (US). **La Paz:** La Paz, 6 Nov. 1984, *M. Nee 30342* (K, NY); in city of La Paz, 18 Nov. 1984, *M. Nee 30396* (BM, CORD, G, K, LP, NY); Inquisivi, along the Chichipata trail betw. San Antonio Hospital & Chichipata, 1 Dec. 1988, *Lewis 881769* (E); Murillo, Calacoto, 22 Oct. 1986, *J. Solomon 15701* (NY, U). **Santa Cruz:** Vallegrande, 10 km (by air) SSE of Vallegrande, on road from Guadalupe to Piraimiri, 31 Jan. 1987, *M. Nee et al. 33909* (NY); 5.5 km S of Vallegrande, vic. Santa Rosita, Quebrada Huasa Cañada, 31 Dec. 1988, *M. Nee & Vargas C. 37477* (NY); Huasacañada, 5 km S de Vallegrande, 1 Oct. 1990, *I. Vargas C. & Vargas C. 753* (NY); Monte Paulo, 4–5 km SE de Piraymirí sobre la carretera a Masicurí, 27 Dec. 1994, *I. Vargas C. & Vargas 3694* (NY); Los Barriales, 28 Feb. 1984, *C. Ochoa & Salas 15536* (US); Caballero, Comarapa, on NW side of town along río Comarapa, 11 Dec. 1992, *M. Nee 43069* (NY). **Tarija:** Arce, 5 km S of comunidad Guayavillas (28.3 km S of Padcaya) on road to Bermejo, 5 May 1983, *J. Solomon 10514* (U); 43 km hacia Padcaya, Huancanqui, 20 Nov. 1986, *S. Beck 14091* (NY). ARGENTINA. **Jujuy:** Dr. M. Belgrano, Mina 9 de octubre, Sierra de Zapla, 21 Nov. 1986, *A. Charpin & Ahumada 20579* (G); Río Lozano, 1 km de la Ruta Nac. 9 sobre el río, 10 Dec. 1998, *O. Morrone et al. 3261* (CORD, SI); Lagunas de Yala, 12/14 Feb. 1971, *A. L. Cabrera et al. 21226* (SI); Quebrada de Yala, 11 Nov. 1978, *A. L. Cabrera et al. 29788* (SI); Mina 9 de Octubre, camino a la antena de TV, 16 Nov. 1980, *A. L. Cabrera et al. 32065* (CORD); Las Escaleras, Mar. 1970, *H. Fabris & Zuloaga 7848* (SI); Zapla, 9 Nov. 1974, *A. Burkart et al. 30618* (SI); Ledesma, on the bank of Río Zora, 25 km NE of Calilegua, 18 Dec. 1938, *W. Eyerdam & Beetle 22617* (G, K); Parque Nacional Calilegua, camino de Abra de Cañas (monolito) hasta el Arroyo Tres Cruces, 3/6 Nov. 1998, *O. Ahumada et al. 8551 & 8773* (CORD, SI); camino a Valle Grande, 18 Oct. 1964, *A. L. Cabrera & Fabris 16123* (SI); Valle Grande, de R. Jordán a Duraznillo (camino a Alto Calilegua), 29 Dec. 1977, *R. Kiesling et al. 1633* (SI); Sierra de Calilegua, Abra Colorada, 8/12 Oct. 1984, *M. Cerana 558* (CORD). **Salta:** Capital, Serranías de San Lorenzo, 27 Oct. 1984, *L. Novara 4338* (G, MCNS); Quebrada de San Lorenzo, 7 Feb. 1939, *E. K. Balls 6071* (K); Chicoana, Quebrada de Escoipe, ruta 33, 12 Mar.1989, *L. Novara 8682* (G, MCNS); Guachipas, Alemania, pedregales del Río Guachipas, 15 Dec. 1929, *S. Venturi 9951* (BM, S); La Caldera, El Ucumar, ruta 9, camino de cornisa a Jujuy, 6 Nov. 1992, *L. Novara & Schiavone 10581* (CORD, MCNS); El Ucumar, 19 Dec. 1998, *H. López 421* (CORD); La Viña, Paraje Entre Ríos, 7 km al W de La Viña sobre el río homónimo, 14 Dec. 1985, *L. Novara 4823* (G, MCNS); Coronel Moldes, en la Ollada, 2 Feb. 1941, *A. T. Hunziker 1182* (CORD); Rosario de Lerma, Ruta San Antonio de los Cobres, km 29, en cruce estación Virrey Toledo, 1 Dec. 1986, *A. Charpin & Novara 20726* (G); Corralito, Río El Manzano, en la Usina, 10 km al S de Campo Quijano, 29 Dec. 1987, *L. Novara 7403* (G, MCNS); Santa Victoria, Los Toldos, Quebrada del Nogalar, 2–5 km al W del pueblo, 19 Apr. 1986, *L. Novara 5247* (G, MCNS); Parque Nacional Baritú, 19 Oct. 1980, *F. Zuloaga et al. 1107* (CORD, SI). **Tucumán:** Capital, Río Salí, 30 Oct. 1921, *S. Venturi 1430* (SI); Famaillá, Río Angostura, 29 Nov. 1946, *B. Sparre 1084* (S); Quebrada Caspinchango, 26 Jan. 1903, *M. Lillo 2947* (G); Monteros, 14 Nov. 1946, *Wall 31* (S); Tafí, Yerba Buena, Jan. 1919, *S. Venturi 58* (SI); camino de Tafí del Valle a El Nogalar, 10 Jan. 1951, *T. Meyer 16371* (E); El Nogalar, camino a Tafí del Valle, 11 Nov. 1952, *A. T. Hunziker 10093* (CORD); Selva Tucumano–Boliviana along Río Los Sosa, ca. 60 km SW of Tucumán, 24 Nov. 1967, *Haas 871* (U); camino a Tafí del Valle, Apeadero Muñoz, km 41, 9 Dec. 1997, *M. Figueroa Romero et al. 1251* (LIL); Siambón, Jan. 1874, *P. G. Lorentz & Hieronymus 899* (CORD, US); Trancas, Tapia, 12 Dec. 1920, *S. Venturi 1090* (SI). **Catamarca:** Belén, 27 Jan. 1936, *Peirano s.n.* (LIL).

The leaf margin in *Solanum fiebrigii* is generally serrulate, but in two specimens (*Steinbach 8803*, *Scolnik & Luti 598*) it is entire. The trichomes in the filaments are scattered, thin, and very transparent and were unobserved by Bitter.

As recorded by Cabrera (1983: 395), the type specimen of *S. fiebrigii* ("Toldos prope Bermejo, juxta rivulum, 1800 m, ...") was collected in Argentinian territory (Prov. Salta, Dpto. Santa Victoria) rather than Bolivia.

The specimen labeled *Lorentz & Hieronymus 899* at Kew, and its photograph at G, do not correspond to any of the syntypes of *S. codonanthum* cited by Bitter, but to *S. lorentzii* Bitter. However, two sheets (A and B) with the same data of collection are deposited at the herbarium of Museo Botánico de Córdoba (CORD), and one at US agrees perfectly with the diagnosis of *S. codonanthum*, as do the photographs of the destroyed Berlin specimen now deposited at F and WIS (Edmonds, pers. comm.).

2. **Solanum sinuatiexcisum** Bitter, Repert. Spec. Nov. Regni Veg. 10: 558. 1912. TYPE: Bolivia. La Paz: "Unduavi, Suryungas," 2800 m, Nov. 1910 (fl, fr), *O. Buchtien 2962* (lectotype, designated here, US!; isotypes, BM!,

K!, LD, NY!, SI!,: Kew negative 8322!, GOET not seen, M not seen, N not seen).

Solanum hyoscyamoides Bitter, Repert. Spec. Nov. Regni Veg. 11: 236. 1912. TYPE: Bolivia. La Paz: Larecaja, "Viciniis Sorata, colle Catarguata, ad rivulum, in umbrosis, in reg. temp.," 2900 m, Oct. 1958 (fl, fr), *G. Mandon 395* (lectotype, designated here, W not seen; isotypes, BM!, G!, K!, P not seen).

Solanum deltoideum Rusby, Descr. S. Amer. pl.: 115. 1920. TYPE: Bolivia. "Yungas," 1890 (fl, fr), *M. Bang 740* (holotype, NY!; isotypes, BM!, G!, GH!, NY!, US!).

Shrub or robust herb, 0.75–2.5 m high, densely viscid-pubescent; stems erect edentate, longitudinally ridged, branches herbaceous, ascending, somewhat viscid but odorless, like the foliage. Leaves solitary or rarely geminate, ovate, the blade (7–)10–16(–22.5) x (4.5–)6–12 cm, the margins coarsely serrate or dentate, with 4 to 10 pairs of unequal teeth directed upward or outward, sinuses broad and slightly profound, apex acuminate, base cuneate to attenuate, both surfaces with long, abundant, and patent glandular trichomes on the midvein and secondary veins, and antrorse trichomes on the lamina; petiole 2–4.5(–6) cm long. Inflorescence extra-axillary, unbranched, cyme umbellate, 4- to 7-flowered; peduncle (1.7–)2–2.8(–4.5) cm long, pedicels 0.7–1.3(–1.5) cm long; calyx 5–8.5(–12) mm long, lobes unequal, narrowly triangular, 1.5 or up to 3 times longer than the tube, 3.5–5.7 mm long; corolla campanulate, 11.5–15 mm long, 10–13 mm diam. at anthesis, white in bud but light purple or blue-violet when open, with dark purple or yellow ring at base within, with abundant non-glandular trichomes on tips and margins; filaments inserted about 1.5–2 mm above the corolla base, their free portion pubescent, as long as or a little longer than the sector fused to the corolla; anthers ellipsoidal, (3.5)4–4.5(–5) mm long, 1–1.2 mm wide, thickened and papillate dorsally and with a connectival prolongation spur-like. Gynoecium ca. 8–10.2 mm long, ovary subglobose, style pubescent on more than basal half, 7.5–9 mm long, extending (1–)2–2.3 mm beyond anthers, stigma saddle-shaped, 0.5 mm long, 0.4 mm wide. Berry globose, 7–10 mm diam., many-seeded (ca. 70), peduncle stout, 2.2–3 cm long, pedicels stout and deflexed, 1.0–1.9 cm long.; pericarp with up to 8 small sclerosomes (0.5–0.8 mm diam.). Seeds 1.5–1.7 x 1.1–1.2 mm. Figures 2, 4C, D, 5A–D, 6.

Distribution and habitat. Solanum sinuatiexcisum is also common in the biogeographical Yungas Province, with a more restricted area to central Bolivia (Depts. Cochabamba, Santa Cruz, and La Paz), and north of Argentina (Prov. Jujuy and Salta), growing from 1500 to 3100 m. It has been collected only once in southern Peru (Dept. Cuzco).

Phenology. Flowering mainly from August to February; fruiting from October to July.

Uses. None registered.

Additional specimens studied. PERU. **Cuzco:** Calca: Vilcabamba, 7 Jan. 1944, *C. Vargas 4016* (US). BOLIVIA. Locality not indicated, *M. Bang 1783* (1781 on label) (BM, G, K, NY, US); Yungas, 1885, *H. Rusby 774* (NY). **Cochabamba:** Ayopaya, Sailapata, Nov. 1935, *M. Cárdenas 3263* (US); Chaparé, Incachaca, 17 Feb. 1929, *J. Steinbach 9201 & 9201 bis,* (G, K, S, U); Incachaca-Chapare, Apr. 1950, *M. Cárdenas 4599* (US); Carrasco, on road from Comarapa to Cochabamba, 4 km W of border with Dpto. Santa Cruz, 10 Feb. 1987, *M. Nee & Solomon 34055* (K, NY); "Churro," 7 km (by air) ESE of Siberia, 8.5 km SW of limit with Dpto. Santa Cruz, 5 Mar. 1988, *M. Nee et al. 36495* (NY); Huertas, Pojos, 1 Nov. 1928, *J. Steinbach 8605* (BM, G, K, NY, S, U); Sacaba, 10 Oct. 1921, *J. Steinbach 5840* (K). **La Paz:** B. Saavedra, Charazani, 20 km hacia Apolo, 5 Aug. 1985, *S. Beck 11375* (NY); Sud Yungas, 12.8 km E of (below) Chuspipata on road to Chulumani, 29 Sep. 1985, *M. Nee & Solomon 32053* (AAU, CORD, G, K, NY); San Felipe, 30 Sep. 1920, *E. Asplund 1092* (UPS); Chungamayo, La Sirena, 31 Aug. 1920, *E. Asplund 303* (UPS); al borde del pueblo de Unduavi (abandonado), 30 Oct. 1986, *S. Beck 11962* (NY); Unduavi, Oct. 1931, *O. Buchtien 9026* (NY); Umgebung von Lambate, 18 June 1980, *T. Feuerer 4496 b* (NY); 5.2 km al SE de Lambate, bosque a lo largo del Rio Chiquilaque Muriyaqui, 12 Jan. 1988, *J. Solomon 17538* (NY); Inquisivi, Jardín Botánico de Quimé, 20 Dec. 1989, *L. Dorr 6727* (AAU, NY); Rio Titi Amaya mouth-Cambillaya, 24 May 1988, *Lewis 88696* (NY); within Quime City limits in a backyard of calle JJ Perez, 23 July 1988, *Lewis 881039* (NY); at the mouth of the Río Chichipata where it meets the Río Khatu, ca. 1 km NE from Quime, 2 Dec. 1988, *Lewis 881786* (NY); along the new Sita–Arcopongo Road where it crosses the Río Sara at Rancho Cuesta Sara, 2 km NE of Sita and 6 km N of Inquisivi, 7 Dec. 1988, *Lewis 882008* (NY); Río Namura, cerca del pueblo de Inquisivi, 14 Jan. 1989, *M. Saldias 649*

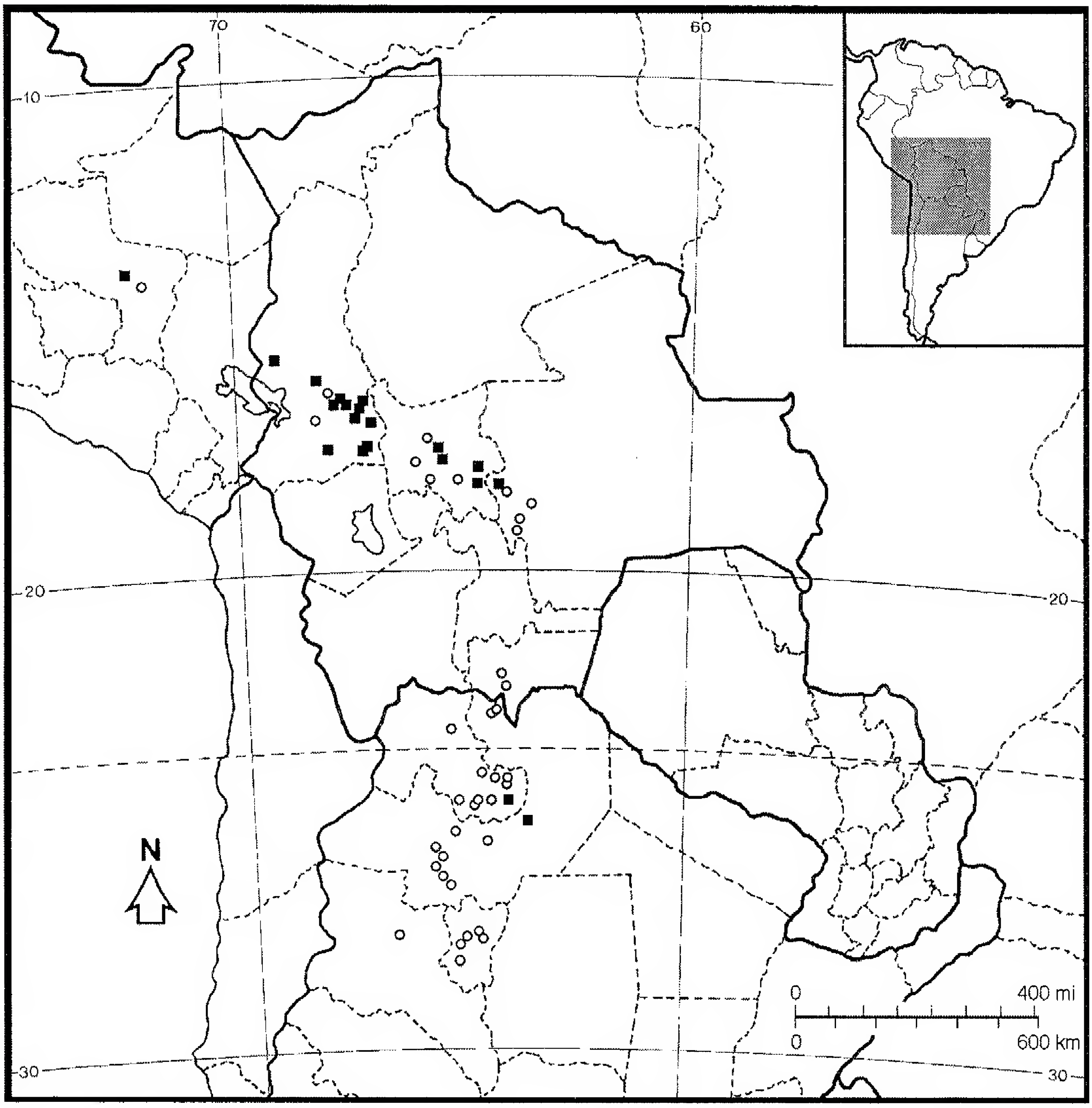
70
60
10
20
20
30
30
N
0
400 mi
0
600 km

Figure 6. Geographic distribution of *Solanum* sect. *Campanulisolanum* based on the collections listed in this paper. Circles = *Solanum fiebrigii*. Squares = *Solanum sinuatiexcisum*.

(NY); Inquisivi, 3 km (by air) and 8 km (by road) SW of Inquisivi, 12 Mar. 1988, *M. Nee & Solomon 36671* (CORD, K, NY); Murillo, 27.4 km N (below) of dam at Lago Zongo, *J. Solomon 8994* (G, NY); Zongo valley, 21 km below the dam at Lago Zongo, 19 Jan. 1985, *J. Solomon 13073* (CORD, G, K, NY); Zongo-Tal, an der Straße nach Cahua 33 km oberhalb des Straßenendes, Weide über Granitschutt, 23 Feb. 1980, *T. Feuerer 8697 a* (NY); Sud Yungas, road from Chulumani to Unduavi via Pte. Villa, ca. 19 km E of Unduavi and 28.9 km W of Pte. Villa, 15 Nov. 1976, *D. Davidson 5019* (US). **Santa Cruz:** Caballero, Parque Nacional Amboro, El Locotal, 5–8 km entrando desde La Siberia, trayecto hacia el Empalme y Khara Huasi, 7 May 1993, *I. Vargas C. et al. 2314* (NY). ARGENTINA. **Jujuy:** Santa Bárbara, Santa Bárbara Range, creek in Quebrada de las Termas, 80 km S of San Pedro, 8 Oct.1938, *W. Eyerdam & Beetle 22469* (K). **Salta:** Anta, PN El Rey, 21 Nov. 1981, *Brown et al. 1693* (MCNS).

When Rusby (1920) described *Solanum deltoideum*, he inexplicably stated "Flowers not seen." We were able to analyze 6 sheets of *Bang 740* (2 at NY and the others at BM, G, GH, and US), all of them with flowers and fruits, that show no differences from *S. sinuatiexcisum.*

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APPENDIX 1

LIST OF SPECIES

1. *Solanum fiebrigii* Bitter

2. *Solanum sinuatiexcisum* Bitter

INDEX TO EXSICCATAE

Examined specimens are listed alphabetically by collector, followed by collection numbers, and a number in parentheses that indicates the species.

Ahumada, O. et al. 8551 (1), 8773 (1); Asplund, E. 303 (2), 1092 (2).

Balls, E. K. 6071 (1); Bang, M. 740 (2), 1783 (2); Beck, S. 11375 (2), 11962 (2), 14091 (1); Bridges, T. s.n. (1); Brooke, W. M. 5851 (1); Brown, et al. 1693 (2); Buchtien, O. 2962 (2), 9026 (2); Burkart, A. et al. 30618 (1).

Cabrera, A. L. & Fabris 16123 (1); Cabrera, A. L. et al. 21226 (1), 29788 (1), 32065 (1); Cárdenas, M. 3263 (2), 3571 (1), 4599 (2), 6087 (1); Cárdenas, M. & Cuteer 7417 (1); Cerana, M. 558 (1); Charpin, A. & Ahumada 20579 (1); Charpin, A. & Novara 20726 (1).

Davidson, D. 5019 (2); Dorr, L. 6727 (2).

Eyerdam, W. & Beetle 22469 (2), 22617 (1).

Fabris, H. & Zuloaga 7848 (1); Feuerer, T. 4496 b (2), 8697 a (2); Fiebrig, K. 2421 (1); Figueroa Romero, M. et al. 1251 (1).

Haas 871 (1); Hunziker, A. T. 1182 (1), 10093 (1).

Kiesling, R. et al. 1633 (1).

Lewis 88696 (2), 881039 (2), 881769 (1), 881786 (2), 882008 (2); Lillo, M. 2947 (1); Lorentz, P. G. & Hieronymus 818 (1), 899 (1).

Mandon, G. 395 (2); Meyer, T. 16371 (1); Morrone O. et al. 3261 (1).

Nee, M. 30342 (1), 30396 (1), 43069 (1); Nee, M. & Solomon 32053 (2), 34055 (2), 36671 (2); Nee, M. & Vargas C. 37477

(1); Nee, M. et al. 33909 (1), 36495 (2); Novara, L. 4338 (1), 4823 (1), 5247 (1), 7403 (1), 8682 (1); Novara, L. & Schiavone 10581 (1); Núñez, P. & Ortega 9158 (1).

Ochoa, C. & Salas 15536 (1).

Peirano s.n. (1).

Rusby, H. 774 (2).

Saldias, M. 649 (2); Scolnik, R. & Luti 598 (1); Solomon, J. 8994 (2), 10514 (1), 13073 (2), 15701 (1), 17538 (2); Sparre, B. 1084 (1); Steinbach, J. 5840 (2), 8605 (2), 8707 (1), 8803 (1), 9201 (2), 9201 bis (2); Steinbach, R. F. 121 (1).

Ugent, D. 4623 (1).

Vargas, C. 4016 (2); Vargas C., I. & Vargas C. 753 (1), 3694 (1); Vargas C., I. et al. 2314 (2); Venturi, S. 58 (1), 1090 (1), 1430 (1), 9951 (1).

Wall 31 (1).

Zuloaga, F. et al. 1107 (1).

FLORISTICS
IN
SOLANACEAE

5

A PRELIMINARY NAMES LIST FOR THE SOLANACEAE OF MESOAMERICA

Sandra Knapp,* Marian Stafford, Mario Sousa-Peña, and Mahinda Martínez

Abstract. In preparation for the treatment of the Solanaceae for *Flora Mesoamericana*, a preliminary list of names is presented here. Information presented for each accepted taxon name includes: original place of publication, basionym, life form, distribution and elevational range in Mesoamerica, and extra-Mesoamerican distribution. The Solanaceae in Mesoamerica are represented by 33 genera and 308 species. This represents a 10% rise in species numbers since the last assessment of the family's diversity in the region. The largest genera are *Solanum*, with 115 species, *Lycianthes*, with 47 species, and *Cestrum*, with 43 species. The great majority of species are native or endemic, and only 30 species are introduced or cultivated. Two endemic genera, not recorded in previous assessments, occur in the region. Species-level endemism is high at 32%; 99 species are endemic to the region. Endemics form two clusters, one in the highlands of Guatemala and southern Mexico, and the other in the highlands of Costa Rica and Panama. The greatest species diversity of Solanaceae occurs in Chiapas state, Mexico, and Costa Rica. Priorities for collecting and for monographic study are briefly discussed.

Key words: distribution, endemism, floristics, Mesoamerica, Solanaceae.

Mesoamerica, the narrow strip of land connecting the continents of North and South America, is one of the last remaining land bridges on the face of the Earth. The area defined here (see Fig. 1) as Mesoamerica comprises the southeastern-most states of Mexico (Chiapas, Tabasco, Yucatán, Campeche, and Quintana Roo) and the seven republics of Central America. This area has traditionally been treated as two separate entities, Mexico and Central America, but floristically it is the heart of tropical North America. Tropical forests occur in Mexico from a little north of the Isthmus of Tehuantepec to the southeast, with small parts of both Oaxaca and Veracruz states covered with these forests. For practical purposes, however, the state boundaries are those used to delimit the phytogeographic area here (see Davidse et al., 1994). The first, and also last, time the flora of Mesoamerica as a whole was treated was in the *Biologia Centrali-Americana* (Hemsley, 1879–1888). *Biologia Centrali-Americana* was an ambitious, privately funded flora and fauna of Mexico and Central America organized by the British naturalists F. DuCane Godman and Osbert Salvin. The work consists of some 67 volumes (published as more than 250 parts), of which botany occupies only five bound volumes, while the beetles alone are treated in 18 bound volumes.

Since that time, the flora of the region has been treated on a national or local basis, with floras of Guatemala, Costa Rica, Panama, Nicaragua, and Veracruz and other states of Mexico either published or in varying stages of completion. The fragmentation of effort across the region and the tendency of earlier taxonomists to describe new taxa from single specimens made the clarification of a regional perspective difficult. The *Flora Mesoamericana* project was begun (see Davidse et al., 1994; Knapp et al., 2000) in order to provide a regional perspective for the floristics of the area and to facilitate regional conservation planning.

Geologically, Mesoamerica can be divided in two. The northern part of the region, from Mexico to mid Nicaragua, is geologically part of the North American continent and is composed of ancient continental crusts, whose form has been more recently affected by volcanic activity (Malfait & Dinkelman, 1972). The southeastern part, southern Nicaragua, Costa Rica, and Panama, is composed of rocks of oceanic origin, uplifted through relatively recent (Pliocene, 3 m.y.a.) tectonic activity (Marshall et al., 1983; Coates, 1997). This geologic complexity, coupled with the bridging nature of the region itself, certainly contributes to its floristic richness. Floristic diversity in the area is high (Williams et al., 1994). Both richness and endemism at the family level are among the largest in the world.

Approximately 18,000 species of flowering plants and ferns are thought to occur in Mesoamerica (Gentry, 1982; Davidse et al., 1994). The two volumes of *Flora Mesoamericana* published to date (Davidse et al., 1994, 1995) contain approximately 7% species new to science (discovered during the lifetime of the project), so the estimate of total species number for the area is likely to rise. Estimates of species endemism for Mesoamerica are relatively low on a global scale (Myers et al., 2000), but this may reflect the relative youth of the region rather than an intrinsically depauperate flora.

Gentry (1982) has characterized Neotropical plant families as being either Amazonian-centered, e.g., Moraceae, Chrysobalanaceae (see Williams et al., 1996), or Andean-centered, e.g., Acanthaceae, Gesneriaceae. In general, families that are Andean-centered have good representation in Mesoamerica, especially in Costa Rica and Panama (Gentry, 1982). These families are primarily epiphytes (or hemiepiphytes), understory shrubs, and "palmetto-type" monocots, and the southeastern part of Mesoamerica is one of the centers of diversity for these groups. The Solanaceae are one such important Andean-centered family (Gentry, 1982; Knapp, 2002a).

The last assessment of the diversity of Solanaceae in Mesoamerica was undertaken by Gentry and D'Arcy in the early 1980s (Gentry & D'Arcy, 1986).

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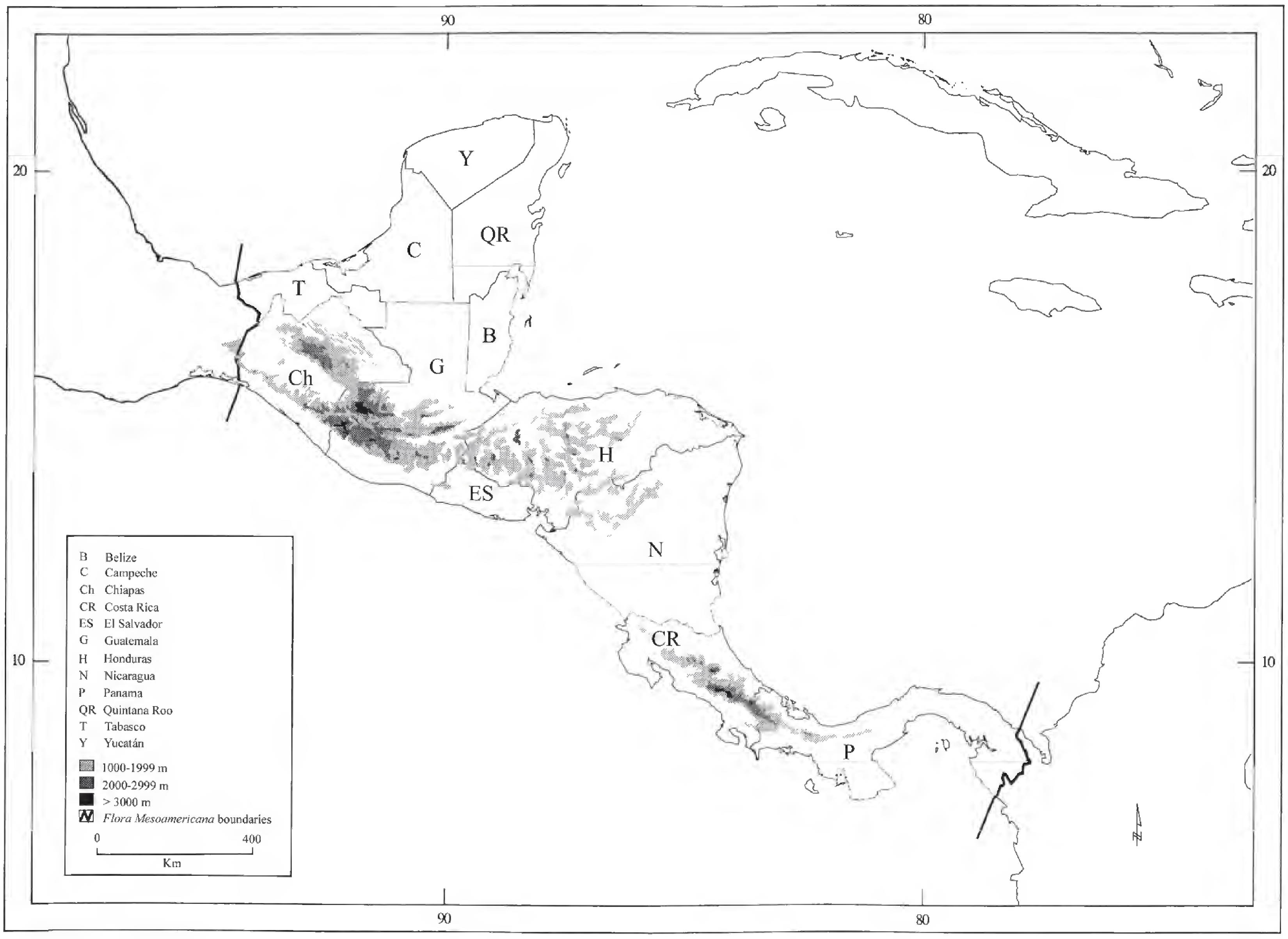
90
80
20
10
Y
C
QR
T
B
G
Ch
H
ES
N
CR
P
B Belize
C Campeche
Ch Chiapas
CR Costa Rica
ES El Salvador
G Guatemala
H Honduras
N Nicaragua
P Panama
QR Quintana Roo
T Tabasco
Y Yucatán
1000-1999 m
2000-2999 m
> 3000 m
Flora Mesoamericana boundaries
0
400
Km

Figure 1. Map of the Flora Mesoamericana area. Abbreviations refer to the geographical divisions recognized by the project.

Their division of the region into the Central American republics and southern Mexico is largely similar to ours, though less detailed within Mexico. At the time of their assessment, the floras of Panama (D'Arcy, 1973 [1974]) and Guatemala (Gentry & Standley, 1974) had been completed, and they relied on the relatively few monographic treatments of solanaceous groups available then (Anderson & Levine, 1982; Carvalho, 1978; Hunziker, 1969; Whalen, 1979; Whalen et al., 1981) and on a few regional or country checklists (Dwyer & Spellman, 1981; Molina R., 1975). They found 272 species in 27 genera, of which 141 species and 1 genus (*Rahowardiana*) were endemic (Gentry & D'Arcy, 1986). The largest genera were *Solanum*, *Lycianthes*, and *Cestrum*, with *Physalis* and *Witheringia* also showing high diversity (see Table 1). The two areas of highest diversity were Guatemala and Costa Rica, with Panama coming a close third.

With the preparation of the *Flora Mesoamericana* account of the Solanaceae, we felt the time was right for a reassessment of the family's diversity in the region. Gentry and D'Arcy (1986) did not present a list of the taxa they accepted for Mesoamerica, even at a provisional level. The names list presented here is preliminary, and as the preparation of generic treatments proceeds, we are certain to discover new distributional records, propose new synonymies, and find species new to science.

ORGANIZATION OF THE LIST

The list is organized alphabetically by genus, and within each genus alphabetically by species. We have included all names accepted in major publications on the Mesoamerican flora, including country floras (Gentry & Standley, 1974; D'Arcy, 1974, 2001), regional or country checklists (Balick et al., 1999; Breedlove, 1986; Dwyer & Spellman,

TABLE 1.

Comparison of species numbers in Gentry and D'Arcy (1986) and this checklist. Numbers in parentheses represent the number of endemics recorded for each category in the two assessments. Genera endemic to Mesoamerica are in bold. Slight differences in total numbers reflect Gentry and D'Arcy's treatment of introduced and cultivated species.

Taxon	Gentry & D'Arcy 1986	This checklist
All taxa	272 (141)	308 (99)
Solanum	102 (39)	115 (23)
Lycianthes	50 (38)	47 (25)
Cestrum	48 (36)	43 (24)
Physalis	20 (1)	25 (4)
Witheringia	11 (9)	13 (7)
Capsicum	3 (0)	7 (0)
Brunfelsia	3 (1)	6 (1)
Nicotiana	1 (1)	5 (0)
Solandra	1 (1)	5 (2)
Brugmansia	—	4 (0)
Datura	2 (0)	4 (0)
Schultesianthus	1 (0)	4 (3)
Cuatresia	2 (1)	3 (1)
Jaltomata	3 (0)	3 (1)
Brachistus	3 (1)	2 (0)
Browallia	2 (0)	2 (0)
Juanulloa	1 (0)	2 (1)
Schwenckia	1 (0)	2 (0)
Tzeltalia	—	2 (2)
Acnistus	1 (0)	1 (0)
Athenaea	1 (0)	*Leucophysalis*
Bouchetia	1 (0)	1 (0)
Chamaesaracha	—	1 (0)
Deprea	1 (0)	*Larnax*
Larnax	—	1 (1)
Leucophysalis	—	1 (0)
Lycium	1 (0)	1 (0)
Margaranthus	—	—
Markea	6 (6)	1 (1)
Melananthus	1 (0)	1 (0)
Merinthopodium	—	1 (1)
Nicandra	1 (0)	1 (0)
Petunia	1 (0)	1 (0)
Plowmania	—	1 (1)
Rahowardiana	1 (1)	*Juanulloa*
Streptosolen	1 (0)	1 (0)

1981; Molina R., 1974, 1975; Haber, 1991; Kappelle et al., 1991; Long & Heath, 1991; Nee, 1986, 1993; Nelson, 1976, 1978, 1986; Reyes-García & Sousa, 1997; Sousa S. & Cabrera C., 1983; Standley, 1930; Standley & Calderón, 1941) and recent systematic works in the family (Barboza & Hunziker, 1989; Bernardello & Hunziker, 1987; Bohs, 1994, 1995; Correll, 1962; Estrada & Martínez, 1999; Hunziker, 1969, 1977, 1987; Knapp, 2000, 2002b; Knapp & Helgason, 1997; Knapp et al., 1997; Martínez, 1998; Nee, 1979, 1991, 1999; Plowman, 1998; Sullivan, 1985; Whalen, 1979, 1984; Whalen et al., 1981). Decisions about synonymy were taken in accordance with our knowledge of the taxa involved and will sometimes differ from those appearing in the literature.

Accepted names appear in bold, and synonyms in italics. Misapplied names or misdeterminations for taxa not occurring in Mesoamerica appear in roman in square brackets and are in most cases accompanied by a note of explanation. For each accepted name, we have included the place of publication, the basionym (if necessary), a brief statement of plant habit, distribution within Mesoamerica using the *Flora Mesoamericana* area codes (see Fig. 1 for detailed explanation), the elevational range in Mesoamerica, and a brief statement of extra-Mesoamerican distribution. Habit and elevation data were taken from both the literature and from herbarium specimens, which we examined systematically in K, BM, MEXU, and MO.

A brief word is required here as to the literature citation of the original place of publication of many names in the large genus *Lycianthes*. The German solanologist Georg Bitter was the last monographer of the genus (Bitter, 1919, 1920), and his treatment was published in the *Abhandlungen herausgeben von Naturwissenschaften Verein zu Bremen* in an issue 24 dated March 1920 (received at BM April 1920, in litt.). A pre-print of his monograph, with the pagination of the journal article, appeared in November 1919 as *Die Gattung Lycianthes* (Bitter, 1919) a few months before the publication of issue 24 of the Abhandlungen. The correct date of valid publication for these names, therefore, should be 1919 in *Die Gattung Lycianthes*, rather than 1920. Citations of the place and date of publication of *Lycianthes* species are often ambiguous (e.g., see D'Arcy, 1973 [1974], 2001). This explicit indication of Bitter's (1919) preprint should go some way to clearing up this confusion and ambiguity in the dates of publication of *Lycianthes* species.

RESULTS AND DISCUSSION

Since the publication by Gentry and D'Arcy (1986) there has been an overall 10% rise in species numbers; this is approximately in line with the published volumes of *Flora Mesoamericana* (see Knapp et al., 2000). It is not surprising that we find higher solanaceous diversity than did Gentry and D'Arcy (1986). This increase is largely due to the success of the collecting program associated with *Flora Mesoamericana*. All of the FM political divisions (see Fig. 1) have increased species numbers. Nowhere is this more clear than in the figures for Chiapas. We record 160 species from Chiapas (see Table 2), more than double the 67 recorded by Gentry and D'Arcy (1986). This dramatic increase reflects the intensive collecting undertaken by D. Breedlove, followed by the publication of a state checklist (Breedlove, 1986) and the more recent intensive collecting undertaken by staff from the Instituto de Biología in the 1980s and 1990s.

In our checklist we record 30 introduced or cultivated non-native species, while Gentry and D'Arcy (1986) recorded 35 such taxa. This in part reflects our inclusion of lowland Tabasco and our better understanding of the distribution of native plants in the Yucatán peninsula. We have also excluded some taxa listed by Gentry and D'Arcy (1986), as we can find no record other than theirs for their occurrence in Mesoamerica (e.g., *Fabiana imbricata* Ruiz & Pav.). We also feel that if a native species is also cultivated locally, it should be recorded as part of the native flora—thus we feel our category is a more accurate assessment of the size of the introduced solanaceous flora.

Mesoamerican Solanaceae occur in all habitats, from seasonally deciduous forest over limestone (Fig. 2A), to dry coastal scrub (Fig. 2B), lowland wet

TABLE 2.

Species diversity and endemicity of Solanaceae by Flora Mesoamericana region and species number by genus for the three largest genera within each region. The number of endemics refers to Mesoamerican (not country) endemicity (see text). Due to distributional overlap, the totals row is the total number of species in each category (for comparison) rather than the total of the column.

FM division	Number of species	Number of endemics	Number of *Solanum*	Number of *Lycianthes*	Number of *Cestrum*
Tabasco	15	0	5	0	0
Chiapas	160	29	60	23	17
Yucatán	46	0	18	2	3
Campeche	18	1	9	2	1
Quintana Roo	31	4	14	0	4
Belize	74	9	34	12	3
Guatemala	181	45	68	29	24
Honduras	125	12	58	14	13
El Salvador	80	5	33	6	11
Nicaragua	122	19	57	14	12
Costa Rica	162	41	74	13	22
Panama	161	43	68	16	23
Total no. of listed species in each category	308	99	115	47	43

forest (Fig. 2C), montane and premontane forests (Fig. 2D, E), and high-elevation oak forests and páramos (Fig. 2F). In general, members of the family are shrubby in habit (often epiphytic or hemiepiphytic, e.g., *Solandra*, *Schultesianthus*) rather than being large canopy trees, and many species are relatively weedy, occurring in secondary disturbed habitats (see Whalen, 1984; Nee, 1999). Other groups, especially *Cestrum* and some species groups of *Solanum* (see D'Arcy, 1973 [1974]; Knapp, 1986, 2002b), are exclusively found in the understory of undisturbed forest and are known from very few collections. More targeted collecting in these habitats will almost certainly improve our understanding of the distribution of these taxa. Gentry and D'Arcy (1986) attempted to quantify the relationships of the Mesoamerican Solanaceae by assessing distribution either into Mexico or into South America. Excluding species found throughout the Neotropics, they discovered that species with Mesoamerican and Mexican ranges were twice as common (53 vs. 26) as those with a Mesoamerican and South American distribution. Our results are similar (Table 3), but care must be taken with this, as further collecting, particularly in Panama, continues to uncover species previously known only from South America (e.g., *Solanum dimorphandrum*, see Knapp, 2000).

Like Gentry and D'Arcy (1986), we find *Solanum*, with 115 species, the largest genus in the family (see Table 1). The increase in numbers of species in *Solanum* is similar to the overall percentage increase in total species numbers, at about 10% (see Table 1). This reflects not only the discovery of new taxa in Mesoamerica, but also the substantial amount of revisionary work in the genus (see above and bibliography for references). *Lycianthes* and *Cestrum*, although in the same order in terms of overall species numbers (see Table 1), both contain fewer species in our list than in Gentry and D'Arcy (1986). In the absence of an explicit species list upon which to base comparisons to Gentry and D'Arcy's (1986) figures, we suggest the decrease in species numbers in these two genera is due firstly to better understanding of synonymy based upon

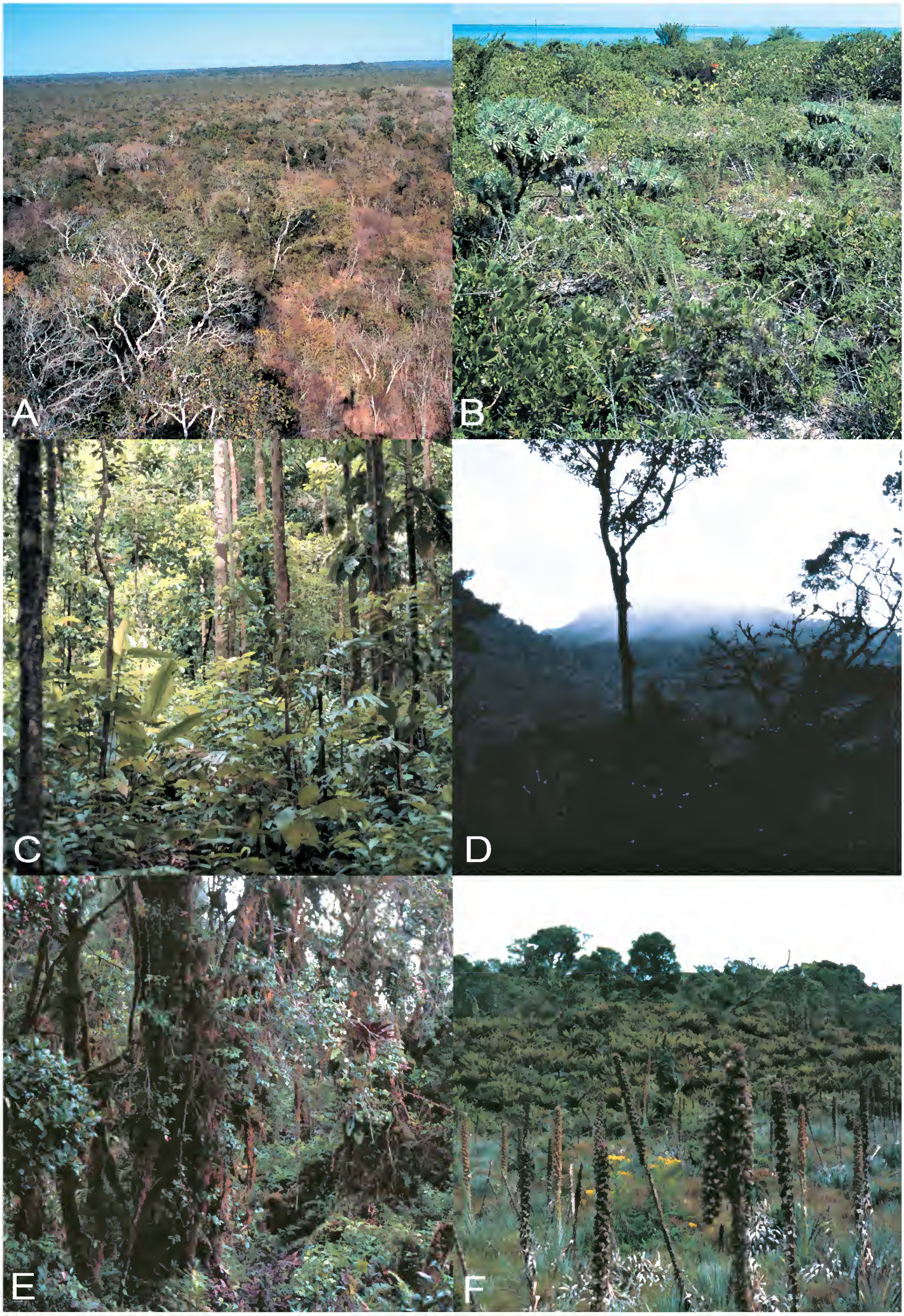

Figure 2. Representative habitats for Solanaceae in Mesoamerica. —A. Seasonally deciduous forest (selva caducifolia) near Calakmul, Campeche state, Mexico. —B. Coastal dunes with *Lycium carolinianum* in the foreground, Xtampu, Yucatán state, Mexico. —C. Understory of wet tropical rainforest (selva alta perennifolia) near Llorona, Parque Nacional Corcovado, Peninsula de Osa, Costa Rica. —D. Cloud-forest-covered slopes of Cerro Pando, border of Costa Rica and Panama. —E. Understory of cloud forest (premontane/montane forests) on Cerro Pando. —F. Oak forest and associated open areas on Cerro de la Muerte, Costa Rica.

TABLE 3.

Numbers of native and introduced taxa recorded in this checklist. Species that occur in Mesoamerica and Mexico, but are not found in South America, are in row 4, while those found only in Mesoamerica and South America, but not in Mexico, are in row 5. Widespread species throughout the Neotropics are excluded (see text).

Category	Number of species
Native (but not endemic)	180
Endemic to Mesoamerica	99
Introduced or cultivated (but not native)	30
Species found in Mexico + Mesoamerica	75
Species found in South America + Mesoamerica	38

the increased specimen base, and secondly upon our more rigorous assessment of misidentifications in the earlier Mesoamerican literature (see particularly *Cestrum* in the list presented here). Species numbers for *Physalis* are broadly similar (see Table 1), but species identities are quite different, based on the recent taxonomic work in the genus (Estrada & Martínez, 1998, 1999; Martínez, 1998, 1999). Some genera recognized by Gentry and D'Arcy (1986) are absent from our list due to generic transfer (see Table 1). Gentry and D'Arcy (1986) recorded a single endemic genus, *Rahowardiana*, now recognized as a species of *Juanulloa* (Knapp et al., 1997). We record two endemic genera (*Plowmania* and *Tzeltalia*, see Table 1), both described (Hunziker & Subils, 1986; Estrada & Martínez, 1998) since the preparation of Gentry and D'Arcy (1986).

Endemism at a local and/or regional level is increasingly important to those setting conservation priorities (Prendergast et al., 1993). For the purposes of the preparation of *Flora Mesoamericana*, endemism is defined as those taxa found only within the FM area, and is not further refined on a country-by-country basis. Endemic species of Solanaceae occur in two major clusters in Mesoamerica. Of the 99 endemic species, only 6 of these are widespread in the region. Thirty-seven endemic species are from the northern part of Mesoamerica (i.e., Chiapas and Guatemala), and 50 species are from Costa Rica and Panama. These clusters correspond with areas of high elevation derived from different geologic sources (see Coates, 1997) and are the same as areas of endemism identified by Gentry and D'Arcy (1986). Endemic species of Solanaceae are overwhelmingly found at middle to high elevations; 66 of the 99 endemic species only grow above 1000 m elevation. Numbers of endemic species are highest between 1000 and 2000 m elevation; of the 66 species only occurring above 1000 m, 25 only grow above 2000 m elevation, while 2/3 of the middle- to high-elevation endemics (41 species) grow between 1000 and 2000 m. This elevational band includes premontane and montane forests (Fig. 2D, E), habitats associated with high species diversity in Andean-centered groups (Gentry, 1982). Endemism in these areas is largely non-overlapping, to be expected in areas of divergent geologic origin. Quite a few species of *Cestrum* are known only from single collections from either Guatemala (e.g., *C. cobanense*) or Costa Rica (e.g., *C. poasanum*) and with further study may prove to be synonyms of other sympatric species. This may reduce the degree of endemism in the Mesoamerican solanaceous flora, but will not obscure the clear bimodality to species richness and endemism in the region.

This preliminary list of the family Solanaceae shows a similar rise in species numbers to that seen for the flora of the region as a whole (ca. 10%: Davidse et al., 1994, 1995; Knapp et al., 2000). It is clear that intensified collecting has increased the specimen base so that realistic assessments of synonymy can now be made, and that also this increase in specimens had brought to light many previously undescribed species. Monographic work has been essential to the clarification of taxon identity, and it is interesting that in those genera in need of modern monographic treatment that endemicity is extremely high and many taxa are known from single collections (e.g., *Cestrum*, *Lycianthes*). These genera are clear priorities for monographic treatment. Many of the endemic species of Solanaceae are from highland regions, both in the north (Guatemala and Chiapas) and the south (Costa Rica and Panama). Further collecting in these species-rich areas will not only result in the discovery of new species, but will be essential in the clarification of synonymy in this complex family. We hope that this names list, by providing an explicit starting point for nomenclature and general species distribution, will stimulate both field collectors to increase the base of Solanaceae specimens and systematists to undertake critical revisions of some key genera. Only in this way will we come to a more complete understanding of the family in an area of its high diversity.

NAMES LIST

33 genera, 2 endemic genera; 308 species, 99 endemic species.

Acnistus Schott

1 species

Acnistus arborescens (L.) Schltdl.
Linnaea 7: 67. 1832.
Atropa arborescens L.
Shrub or treelet
Ch, G, H, N, CR, P
400–2000 m
Native (S Mexico, West Indies, South America)

Acnistus coccoloboides Dammer = **Witheringia coccoloboides** (Dammer) Hunz.

Acnistus lehmanni Dammer = **Witheringia solanacea** L'Hér.

Acnistus macrophyllus (Benth.) Standl. = **Acnistus arborescens** (L.) Schltdl.

Athenaea affinis C. V. Morton = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Athenaea cernua Donn. Sm. = **Chamaesaracha cernua** (Donn. Sm.) Hunz.

Athenaea locuples Standl. & Steyerm. = **Brachistus stramoniifolius** (Kunth) Miers

Athenaea nelsonii Fernald = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Athenaea sylvarum Standl. & C. V. Morton = **Larnax sylvarum** (Standl. & C. V. Morton) Sawyer

Athenaea viscida (Standl.) Standl. & Steyerm. = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Athenaea viscosa (Schrad.) Fernald = **Leucophysalis viscosa** (Schrad.) Hunz.

Atropa arborescens L. = **Acnistus arborescens** (L.) Schltdl.

Atropa physalodes L. = **Nicandra physalodes** (L.) Gaertn.

Atropa procumbens Cav. = **Jaltomata procumbens** (Cav.) J. L. Gentry

Bassovia donnell-smithii J. M. Coult. = **Brachistus stramoniifolius** (Kunth) Miers

Bassovia escuintlensis (J. M. Coult.) Standl. = **Lycianthes heteroclita** (Sendtn.) Bitter

Bassovia macrophylla (Kunth) J. M. Coult. = **Witheringia solanacea** L'Hér.

Bassovia mexicana B. L. Rob. = **Witheringia mexicana** (B. L. Rob.) Hunz.

Bassovia stramoniifolia (Kunth) Standl. = **Brachistus stramoniifolius** (Kunth) Miers

Bouchetia Dunal

1 species

Bouchetia erecta Dunal
in DC., Prodr. 13(1): 589. 1852.
Herb
Ch, G
1400–1600 m
Native (SW U.S.A., Mexico)

Brachistus Miers

2 species

Brachistus affinis (C. V. Morton) D'Arcy, J. L. Gentry & Averett = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Brachistus ceratocalycius Donn. Sm. = **Lycianthes ceratocalycia** (Donn. Sm.) Bitter

Brachistus fuscoviolaceus Cufod. = **Witheringia coccoloboides** (Dammer) Hunz.

Brachistus hebephyllus Miers = **Witheringia solanacea** L'Her.

Brachistus lanceolatus Greenm. = **Capsicum lanceolatum** (Greenm.) C. V. Morton & Standl.

Brachistus macrophyllus (Dunal) Miers = **Witheringia solanacea** L'Hér.

Brachistus meianthus Donn. Sm. = **Witheringia meiantha** (Donn. Sm.) Hunz.

Brachistus nelsonii (Fernald) D'Arcy, J. L. Gentry & Averett
Ann. Missouri Bot. Gard. 68: 227. 1981.
Athenaea nelsonii Fernald
Shrub
T, C, Ch, C, B, G, H, CR, P
100–1000 m
Native (S Mexico)

Brachistus poasensis Cufod. = **Witheringia coccoloboides** (Dammer) Hunz.

Brachistus solanaceus (L'Hér.) Hemsl. = **Witheringia solanacea** L'Hér.

Brachistus stramoniifolius (Kunth) Miers
Ann. Mag. Nat. Hist. ser. 2, 3(16): 263. 1849.
Witheringia stramoniifolia Kunth
Herb, shrub, or tree
T, Ch, G, H, ES, N, CR, P
300–2000 m
Native (Mexico, N South America)

Browallia L.

2 species

Browallia americana L.
Sp. Pl. 631. 1753.
Herb or subshrub
Ch, G, H, ES, N, CR, P
0–2300 m
Native and cultivated (S Mexico, South America, West Indies)

Browallia jamesonii Benth. = **Streptosolen jamesonii** (Benth.) Miers

Browallia speciosa Hook. f.
Bot. Mag. 73: t. 4339. 1947.
Herb
H, CR, P
1400–2100 m
Native (N South America)

Browallia viscosa Kunth = **Browallia americana** L.

Brugmansia Pers.

4 species

Brugmansia×candida Pers.
Syn. Pl. 1: 216. 1805.
Shrub or treelet
Ch, B, G, H, ES, N, P
400–2500 m
Introduced and cultivated (both parents native to N South America)

Brugmansia sanguinea (Ruiz & Pav.) D. Don
Brit. Fl. Gard. 3: t. 272. 1835.
Datura sanguinea Ruiz & Pav.
Shrub, treelet, or tree
H, CR
ca. 2300 m
Introduced and cultivated (native to Colombia, Ecuador, Peru, Bolivia)

Brugmansia suaveolens (Willd.) Bercht. & J. Presl
Prir. Rostlin 1: Solanac. 45. 1823.
Datura suaveolens Willd.
Shrub or treelet
Ch, Y, G, H, ES, N, CR, P
600–2000 m
Introduced and cultivated (native to Brazil; widely cultivated in tropical areas)

Brugmansia versicolor Lagerh.
Bot. Jahrb. Syst. 20: 666. 1895.
Shrub or treelet
Ch
Altitude unknown
Introduced and cultivated (native to Ecuador; widely cultivated)

Brunfelsia L.

6 species; 1 endemic species

Brunfelsia americana L.
Sp. Pl. 191. 1753.
Shrub
Y, H
0 m
Introduced and cultivated (native to Jamaica, Antilles)

Brunfelsia chocoensis Plowman
Bot. Mus. Leafl. 23: 245, t. 14. 1973.
Shrub
P
0–200 m
Native (Colombia)

Brunfelsia dwyeri D'Arcy
Ann. Missouri Bot. Gard. 57: 259. 1971.
Shrub or tree
P
700–1000 m
Endemic

Brunfelsia grandiflora D. Don
Edinburgh New Philos. J. 7: 86. 1829.
Shrub or tree
H, N, CR, P
0–1500 m
Introduced and cultivated (native to E slopes of the Andes)

[Brunfelsia latifolia (Pohl) Benth.]
Recorded from Honduras by Molina R. (1975: 98) as a cultivated species. Possibly a misdetermination for *B. grandiflora. Brunfelsia latifolia* is rarely cultivated, but the name has been commonly used in the horticultural trade for *B. grandiflora* and *B. australis* Benth.

Brunfelsia nitida Benth.
in DC., Prodr. 10: 201. 1846.
Shrub or treelet
Ch, Y, G
0–100 m
Cultivated (native of the West Indies)

Brunfelsia nyctaginoides Standl. = **Plowmania nyctaginoides** (Standl.) Hunz. & Subils

Brunfelsia undulata Sw.
Nov. Gen. Sp. 90. 1788.
Shrub or tree
H, N, P
0–200 m
Introduced and cultivated (Jamaica)

Capsicum L.

7 species

Capsicum annuum var. *annuum* = **Capsicum annuum** L.
Capsicum annuum var. *aviculare* (Dierb.) D'Arcy & Eshbaugh = **Capsicum annuum** L.

Capsicum annuum L.
Sp. Pl. 188. 1753.
Herb, subshrub, or shrub
T, Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–1200 m
Native and cultivated (S U.S.A., Mexico, N South America, West Indies)

Capsicum annuum var. *conoides* (Mill.) Irish = **Capsicum annuum** L.

Capsicum annuum var. *glabriusculum* (Dunal) Heiser & Pickersgill = **Capsicum annuum** L.

Capsicum annuum var. *minimum* (Mill.) Heiser = **Capsicum annuum** L.

Capsicum asterotrichum Standl. = **Witheringia asterotricha** (Standl.) Hunz.

Capsicum baccatum L.
Mant. Pl. 47. 1767.
Herb or subshrub
B, ES
Low elevations

Native and cultivated (Neotropics, native only in South America S of the Amazon Basin)

Capsicum chinense Jacq.
Hort. Bot. Vindob. 3: 38, t. 67. 1776.
Herb or shrub
B, P
700–900 m
Cultivated (cultivated from S U.S.A. to Chile)

Capsicum ciliatum (Kunth) Kuntze = **Capsicum rhomboideum** (Dunal) Kuntze

Capsicum costaricense Standl. & C. V. Morton = **Witheringia solanacea** L'Hér.

Capsicum frutescens L.
Sp. Pl. 189. 1753.
Herb or subshrub
Ch, Y, QR, B, G, H, ES, P
Altitude unknown
Native (?) and cultivated (S U.S.A, Mexico to South America, West Indies)

Capsicum frutescens var. *baccatum* (L.) Irish = **Capsicum frutescens** L.

Capsicum fuscoviolaceum (Cufod.) C. V. Morton & Standl. = **Witheringia coccoloboides** (Dammer) Hunz.

Capsicum isothrix Standl. = **Witheringia solanacea** L'Hér.

Capsicum lanceolatum (Greenm.) C. V. Morton & Standl.
Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 272. 1940.
Brachistus lanceolatus Greenm.
Subshrub, shrub, or treelet
Ch, G, H
500–2000 m
Native (S Mexico)

Capsicum lundellii C. V. Morton = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Capsicum maculatum C. V. Morton & Standl. = **Witheringia maculata** (C. V. Morton & Standl.) Hunz.

Capsicum macranthum Standl. & C. V. Morton = **Witheringia macrantha** (Standl. & C. V. Morton) Hunz.

Capsicum macrophyllum (Dunal) Standl. = **Witheringia solanacea** L'Hér.

Capsicum malacophyllum Standl. = **Brachistus stramoniifolius** (Kunth) Miers

Capsicum meianthum (Donn. Sm.) Standl. & Steyerm. = **Witheringia meiantha** (Donn. Sm.) Hunz.

Capsicum multiflorum Standl. & C. V. Morton = **Witheringia asterotricha** (Standl.) Hunz.

Capsicum pringlei (S. Watson) J. F. Macbr. & Standl. = **Capsicum rhomboideum** (Dunal) Kuntze

Capsicum pubescens Ruiz & Pav.
Fl. Peruv. 2: 30. 1799.
Herb or shrub
Ch, B, G, H, CR
0–2000 m
Introduced and cultivated (native of Andean South America)

Capsicum rhomboideum (Dunal) Kuntze
Revis. Gen. Pl. 2: 450. 1891.
Witheringia rhomboidea Dunal
Herb, subshrub, or shrub
Ch, G, H, ES, N, CR
100–1700 m
Native (Mexico to Peru)

Capsicum silvigaudens Standl. & L. O. Williams = **Witheringia meiantha** (Donn. Sm.) Hunz.

Capsicum solanaceum (L'Hér.) Kuntze = **Witheringia solanacea** L'Hér.

Capsicum solanaceum var. *glabrescens* Kuntze = **Witheringia solanacea** L'Hér.

Capsicum solanaceum var. *macrophylla* (Dunal) Kuntze = **Witheringia solanacea** L'Hér.

Capsicum solanaceum var. *pubescens* Kuntze = **Witheringia asterotricha** (Standl.) Hunz.

Capsicum stenophyllum C. V. Morton & Standl. = **Witheringia meiantha** (Donn. Sm.) Hunz.

Capsicum stramoniifolium (Kunth) Kuntze = **Brachistus stramoniifolius** (Kunth) Miers

Capsicum stramoniifolium (Kunth) Standl. = **Brachistus stramoniifolius** (Kunth) Miers

Capsicum subulatum Standl. & C. V. Morton = **Brachistus stramoniifolius** (Kunth) Miers

Capsicum tetramerum Standl. & C. V. Morton = **Witheringia solanacea** L'Hér.

Capsicum viscidum Standl. = **Brachistus nelsonii** (Fernald) D'Arcy, J. L. Gentry & Averett

Cestrum L.

43 species; 24 endemic species
Cestrum acuminatum Francey
Candollea 6: 348. 1935.
Shrub or treelet
CR, P
1400–2100 m
Endemic

Cestrum alternifolium (Jacq.) O. E. Schulz
in Urb., Symb. Antill. 6: 270. 1909.
Ixora alternifolia Jacq.
Shrub or tree
Y, QR, G, H, ES, N, CR, P
0–800 m
Native (S Mexico, N South America, West Indies)

Cestrum anagyris Dunal = **Cestrum laxum** Benth.

Cestrum aurantiacum Lindl.
Edward's Bot. Reg. 30 (Misc.): 71. 1844.
Shrub or tree
Ch, G, H, ES, N, CR, P
700–2600 m
Native (S Mexico)

Cestrum baenitzii Lingelsh. = **Cestrum megalophyllum** Dunal

Cestrum chiapense Brandegee = **Cestrum regelii** Planch.

Cestrum chiriquianum Francey
Candollea 6: 96. 1935.
Shrub
CR, P
1200–3500 m
Endemic

Cestrum cobanense Francey
Candollea 6: 372. 1935.
Shrub
G
ca. 1500 m
Endemic

Cestrum costaricense Francey
Candollea 6: 368. 1935.
Habit unknown
CR, P?
300–3000 m
Endemic
Of uncertain application, as both syntypes were destroyed

Cestrum dasyanthum Donn. Sm.
Bot. Gaz. 23: 11. 1897.
Shrub
G
2300–3000 m
Endemic

Cestrum diurnum L.
Sp. Pl. 191. 1753.
Shrub
Ch, Y, QR
0 m
Native and cultivated (SE U.S.A. (?), Mexico, West Indies; widely cultivated in tropics and subtropics)

Cestrum donnell-smithii Francey = **Cestrum microcalyx** Francey

Cestrum dumetorum Schltdl.
Linnaea 7: 61. 1832.
Shrub or treelet
G, H, ES, N, CR
400–1500 m
Native (Mexico)

Cestrum elegantissimum C. V. Morton
J. Arnold Arbor. 17: 347. 1936.

Shrub
Ch, G
1200–2000 m
Endemic

Cestrum evanidum C. V. Morton
J. Arnold Arbor. 17: 346. 1936.
Shrub or treelet
G
1300–1600 m
Endemic

Cestrum flavescens Greenm.
Proc. Amer. Acad. Arts 34: 72. 1899.
Shrub or treelet
Ch
950–1200 m
Native? (Mexico)
Accepted name in Breedlove (1986), but may not occur in Mesoamerica; all BM (and type) specimens are from much further north in Central Mexico.

Cestrum formosum C. V. Morton
J. Arnold Arbor. 17: 348. 1936.
Shrub
Ch, G
2600–3200 m
Endemic

Cestrum fragile Francey
Candollea 7: 27. 1936.
Shrub, treelet, or tree
N, CR, P
800–1500 m
Endemic

Cestrum fragile var. *grandiflorum* C. V. Morton = **Cestrum fragile** Francey

Cestrum franceyi C. V. Morton
J. Arnold Arbor. 17: 345. 1936.
Shrub
G
ca. 1150 m
Endemic
Replacement name for *C. pedunculatum* Francey

Cestrum fraternum C. V. Morton
J. Arnold Arbor. 17: 345. 1936.
Shrub
Ch, G
2300–3000 m
Endemic

Cestrum glanduliferum Kerber ex Francey
Candollea 6: 386. 1935.
Shrub, treelet, or tree
Ch, G, H, N, CR, P
0–1000 m
Native (E Mexico)

[Cestrum glandulosum Francey]
Accepted name in Reyes-García & Sousa (1997)–probably a misprint for *C. glanduliferum* Kerber ex Francey; *C. glandulosum* Francey does not exist.

Cestrum gracile Francey
Candollea 6: 368. 1935.
Habit unknown
P
Endemic
Only known from the destroyed type–name of uncertain application

Cestrum guatemalense Francey
Candollea 6: 98. 1935.
Shrub or treelet
Ch, G, H, ES
1900–3800 m
Endemic

Cestrum guatemalense var. *gracile* C. V. Morton = **Cestrum guatemalense** Francey

Cestrum irazuense Kuntze
Revis. Gen. Pl. 2: 450. 1891.
Shrub or treelet
CR
2000–3000 m
Endemic

Cestrum jacaltenanginum var. *tomentosum* Francey = **Cestrum regelii** Planch.

Cestrum johnniegentrianum D'Arcy
Ann. Missouri Bot. Gard. 60: 601. 1973 [1974].
Shrub
P
700–1000 m
Endemic

Cestrum lanatum M. Martens & Galeotti = **Cestrum tomentosum** L. f.

Cestrum langeanum D'Arcy
Ann. Missouri Bot. Gard. 60: 603. 1973 [1974].
Shrub
P
300–1000 m
Endemic

Cestrum latifolium Lam.
Tabl. Encycl. 2: 5, no. 2275. 1794.
Shrub or tree
G, P
0–100 m
Native (Guayanas, Peru, Brazil, Venezuela, Antilles)

[Cestrum laurifolium L'Hér.]
Accepted name in Standley & Calderón (1941: 192)–a Caribbean species, misapplied for *Cestrum megalophyllum* Dunal.

Cestrum laxum Benth.
Pl. Hartw.: 23. 1839.
Shrub or treelet
Ch, G, H
2220–3000 m
Native (S Mexico)

Cestrum lewisii D'Arcy = **Cestrum acuminatum** Francey

Cestrum luteo-virescens Francey
Candollea 6: 349. 1935.
Shrub or treelet
Ch, G, ES
1200–2200 m
Native (S Mexico)

[Cestrum macrophyllum Vent.]
Recorded from Honduras by Molina R. (1975: 98). A Caribbean species–possibly a misidentification of *C. megalophyllum* or *C. diurnum*.

Cestrum mariquitense Kunth
Nov. Gen. Sp. 3: 57. 1818.
Shrub or treelet
CR, P
100–600 m
Native (South America to Paraguay and Corrientes in Argentina)

Cestrum mariquitense var. *latifolium* Standl. & C. V. Morton = **Cestrum mariquitense** Kunth

Cestrum megalophyllum Dunal
in DC., Prodr. 13(1): 638. 1852.
Shrub or tree
Ch, B, G, H, ES, N, CR, P
0–2000 m
Native (S Mexico, N South America to Bolivia and Brazil, West Indies)
There is likely to be an earlier name for this widespread species–*Cestrum schlechtendahlii* G. Don may be the older, correct name, fide M. Nee.

Cestrum mexicanum Francey = **Cestrum guatemalense** Francey

Cestrum microcalyx Francey
Candollea 6: 301. 1936.
Shrub or treelet
N, CR, P
0–1800 m
Native (N South America to Bolivia)

Cestrum mortonianum J. L. Gentry
Phytologia 26: 267. 1973.
Treelet
Ch, G
2300–2500 m
Endemic

Cestrum nitidum M. Martens & Galeotti
Bull. Acad. Roy. Sci. Bruxelles 12: 147. 1845.
Shrub or treelet
Ch
1800 m
Native (S Mexico)

Cestrum nocturnum L.
Sp. Pl. 191. 1753.
Shrub or tree
Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–1800 m
Native (Mexico, extensively cultivated in the West Indies)

Cestrum pacayense Francey
Candollea 6: 90. 1935.
Shrub
G, H, ES
1800–3300 m
Endemic

Cestrum pittieri Francey = **Cestrum glanduliferum** Francey

Cestrum poasanum Donn. Sm.
Bot. Gaz. 33: 253. 1902.
Shrub
CR
ca. 1050 m
Endemic

Cestrum racemosum Ruiz & Pav.
Fl. Peruv. 2: 29, t. 154. 1799.
Shrub or tree
Ch, B, G, H, ES, N, CR, P
0–2300 m
Native (S Mexico, N South America to Bolivia)

Cestrum reflexum Sendtn.
in Mart., Fl. Bras. 10: 218. 1846.
Shrub or vine
N, CR, P
0–400 m
Native (South America as far S as Bolivia and Paraguay)

Cestrum regelii Planch.
Fl. Serres Jard. Eur. 9: 229, t. 946. 1854.
Shrub
Ch, G, P
1500–2000 m
Endemic

Cestrum rugulosum Francey
Candollea 7: 78. 1936.
Shrub
CR, P
1500–2500 m
Endemic

Cestrum scandens Vahl
Eclog. Amer. 1: 24. 1797.
Shrub or vine
Ch, QR, G, H, ES, N, CR, P
0–900 m
Native (S Mexico, Colombia, Venezuela, Ecuador)

Cestrum skutchii C. V. Morton
J. Arnold Arbor. 17: 347. 1936.
Shrub
G, H
1500–1700 m
Endemic

Cestrum standleyi Francey
Candollea 6: 249. 1935.
Shrub or treelet
CR, P
400–2500 m
Endemic

Cestrum strigilatum Ruiz & Pav.
Fl. Peruv. 2: 29, t. 156. 1799.
Shrub or treelet
CR, P
0–600 m
Native (South America)

Cestrum terminale Francey, nom. illegit. = **Cestrum scandens** Vahl

Cestrum tomentosum L. f.
Suppl. Pl. 150. 1782.
Shrub or treelet
Ch, G, H, ES, N, CR, P
500–2400 m
Native (Mexico, Andean South America)

Cestrum valerioi Francey
Candollea 6: 93. 1935.
Shrub or treelet
CR
2700–3000 m
Endemic

[Cestrum warscewiczii var. macrocalyx Francey]
Accepted name in Breedlove (1986). Not a validly published name; may refer to *Cestrum aurantiacum* var. *macrocalyx* Francey = *C. aurantiacum*.

Cestrum warszewiczii Klotzsch = **Cestrum aurantiacum** Lindl.

Cestrum yucatanense Francey = **Cestrum nocturnum** L.

Chaetochilus lateriflorus Vahl = **Schwenckia lateriflora** (Vahl) Carvalho

Chamaesaracha (A.Gray) Benth.

1 species

Chamaesaracha cernua (Donn. Sm.) Hunz.
Contr. Gray Herb. 210: 25. 1980.
Athenaea cernua Donn. Sm.
Herb
Ch, B, G
200–900 m
Native (Mexico)

Cuatresia Hunz.

3 species; 1 endemic species

Cuatresia exiguiflora (D'Arcy) Hunz.
Opera Bot. 92: 75. 1987.
Witheringia exiguiflora D'Arcy
Shrub or treelet
N, CR, P
0–500 m
Native (N South America)

Cuatresia riparia (Kunth) Hunz.
Kurtziana 10: 20. 1977.
Witheringia riparia Kunth
Subshrub, shrub, treelet, or tree
B, G, CR, P
0–2100 m
Native (N South America)

Cuatresia sp. (aff. *fosteriana* Hunz.)
Shrub
CR, P
1700–2100 m
Endemic
Under study by Sousa-Peña; not *C. plowmanii* Hunz. or *C. foreroi* Hunz. of South America.

Cyphomandra allophylla (Miers) Hemsl. = **Solanum allophyllum** (Miers) Standl.

Cyphomandra betacea (Cav.) Sendtn. = **Solanum betaceum** Cav.

Cyphomandra costaricensis Donn. Sm. = **Solanum rojasianum** (Standl. & Steyerm.) Bohs

Cyphomandra diversifolia (Dunal) Bitter = **Solanum diversifolium** Dunal

Cyphomandra diversifolia subsp. *chlorantha* (Rusby) Bohs = **Solanum diversifolium** Dunal

Cyphomandra dolichocarpa Bitter = **Solanum fortunense** Bohs

Cyphomandra hartwegii (Miers) Walp. = **Solanum circinatum** Bohs

Cyphomandra mollicella Standl. = **Solanum circinatum** Bohs

Cyphomandra rojasiana Standl. & Steyerm. = **Solanum rojasianum** (Standl. & Steyerm.) Bohs

Datura L.

4 species

Datura candida (Pers.) Saff. = **Brugmansia×candida** Pers.

Datura discolor Bernh.
Neues J. Pharm. Aerzte 26: 149. 1833 & Linnaea 8: 138. 1833.
Herb
Y
0 m
Native (SW U.S.A., Mexico)

Datura fastuosa L. = **Datura metel** L.

Datura inoxia Mill.
Gard. Dict. ed. 8, Datura no. 5. 1768.
Herb
Y, QR, G, H, ES, N
0–900 m
Native and cultivated (native of Mexico; U.S.A., South America, West Indies)

Datura maxima Sessé & Moç. = **Solandra maxima** (Sessé & Moç.) P. S. Green

Datura metel L.
Sp. Pl. 179. 1753.
Shrub
Ch, H, ES, P
0–900 m
Introduced and cultivated (probably native of Mexico; worldwide)

Datura meteloides Dunal = **Datura inoxia** Mill.

[Datura pruinosa Greenm.]
Accepted name in Gentry & Standley (1974), probable misidentification; this species does not occur in Mesoamerica (R. Bye, pers. comm.).

[Datura quercifolia Kunth]
Recorded from Honduras by Molina R. (1975). Misdetermination–this species only occurs in Mexico.

Datura sanguinea Ruiz & Pav. = **Brugmansia sanguinea** (Ruiz & Pav.) D. Don

Datura stramonium L.
Sp. Pl. 179. 1753.
Herb or shrub
Ch, Y, B, G, H, ES, CR, P
800–2500 m
Native (U.S.A., Mexico, South America, West Indies, Old World)

Datura suaveolens Willd. = **Brugmansia suaveolens** (Willd.) Bercht. & J. Presl

[Deprea orinocensis (Kunth) Raf.]
Accepted name in D'Arcy (1973 [1974]). Misapplied for *Larnax sylvarum* (Standl. & C. V. Morton) Sawyer.

Deprea sylvarum (Standl. & C. V. Morton) Hunz. = **Larnax sylvarum** (Standl. & C. V. Morton) Sawyer

Ixora alternifolia Jacq. = **Cestrum alternifolium** (Jacq.) O. E. Schulz

Jaltomata Schltdl.
3 species; 1 endemic species

Jaltomata confinis (C. V. Morton) J. L. Gentry
Phytologia 27: 286. 1973.
Saracha confinis C. V. Morton
Herb
G
2400–3800 m
Endemic

Jaltomata procumbens (Cav.) J. L. Gentry
Phytologia 27: 287. 1973.
Atropa procumbens Cav.
Herb
Ch, B, G, H, ES, N, CR, P
600–2500 m
Native (SW U.S.A., Mexico, South America)

Jaltomata repandidentata (Dunal) Hunz.
Kurtziana 10: 8. 1977.
Saracha procumbens var. *repandidentata* Dunal
Herb, subshrub, or shrub
G, ES, N, CR
200–1000 m
Native (Mexico, South America)

Juanulloa Ruiz & Pav.
2 species; 1 endemic species

Juanulloa mexicana (Schltdl.) Miers
Ann. Mag. Nat. Hist. ser. 2, 4: 188. 1849.
Laureria mexicana Schltdl.
Epiphytic or hemiepiphytic shrub or vine
Ch, G, H, CR, P
300–1000 m
Native (S Mexico, Colombia)

Juanulloa panamensis Miers = **Juanulloa mexicana** (Schltdl.) Miers

Juanulloa wardiana (D'Arcy) S. Knapp
Novon 5: 283. 1995.
Rahowardiana wardiana D'Arcy
Epiphytic or hemiepiphytic shrub
P
0–900 m
Endemic

Laureria mexicana Schltdl. = **Juanulloa mexicana** (Schltdl.) Miers

Larnax Miers

1 species; 1 endemic species

Larnax sylvarum (Standl. & C. V. Morton) Sawyer
Novon 11: 461. 2001.
Athenaea sylvarum Standl. & C. V. Morton
Herb, subshrub, or shrub
CR, P
Endemic

Leucophysalis Rydb.

1 species

Leucophysalis viscosa (Schrad.) Hunz.
Kurtziana 21: 283. 1991.
Saracha viscosa Schrad.
Herb
Ch, G
ca. 2000 m
Native (Mexico)

Lycianthes (Dunal) Hassl.

47 species; 25 endemic species

Lycianthes acapulcensis (Baill.) D'Arcy
Solanaceae Newslett. 2: 23. 1986.
Parascopolia acapulcensis Baill.
Herb
G, H, ES, N
0–100 m
Native (Mexico)
Often misidentified as *L. ciliolata* (M. Martens & Galeotti) Bitter

Lycianthes acidochondra (Bitter) Bitter
Die Gattung Lycianthes 341. 1919.
Solanum acidochondrum Bitter
Vine
P
800–1000 m
Endemic

Lycianthes amatitlanensis (J. M. Coult. & Donn. Sm.) Bitter
Die Gattung Lycianthes 441. 1919.
Solanum amatitlanense J. M. Coult. & Donn. Sm.
Herb or subshrub
Ch, G, H, N, CR, P
200–1100 m
Endemic

Lycianthes anomala Bitter
Die Gattung Lycianthes 514. 1919.
Shrub or tree
N
(200–)900–1000 m
Native (S Mexico)

Lycianthes armentalis J. L. Gentry
Phytologia 26: 269. 1973.
Shrub
Ch, Y, C, QR, B, G
0–1000 m
Native (S Mexico)

Lycianthes arrazolensis (J. M. Coult. & Donn. Sm.) Bitter
Die Gattung Lycianthes 388. 1919.
Solanum arrazolense J. M. Coult. & Donn. Sm.
Herb or shrub
Ch, G, H, N, CR
900–3000 m
Native (Mexico)

Lycianthes austin-smithii C. V. Morton & Standl. = **Witheringia cuneata** (Standl.) Hunz.

Lycianthes barbatula Standl. & Steyerm.
Field Mus. Nat. Hist., Bot. Ser. 23: 228. 1947.
Shrub
G
1200–2600 m
Endemic

Lycianthes beckneriana D'Arcy
Ann. Missouri Bot. Gard. 60: 635. 1973 [1974].
Tree or vine
P
1000–1800 m
Endemic

Lycianthes ceratocalycia (Donn. Sm.) Bitter
Die Gattung Lycianthes 498. 1919.
Brachistus ceratocalycius Donn. Sm.
Shrub

Ch, G
1500–1800 m
Endemic

Lycianthes chiapensis (Brandegee) Standl.
Field Mus. Nat. Hist., Bot. Ser. 11: 173. 1936.
Solanum chiapense Brandegee
Shrub or vine
Ch, G, N
800–2400 m
Native (S Mexico)

Lycianthes chiriquensis Standl. = **Witheringia cuneata** (Standl.) Hunz.

Lycianthes ciliolata (M. Martens & Galeotti) Bitter
Die Gattung Lycianthes 410. 1919.
Solanum ciliolatum M. Martens & Galeotti
Herb
Ch, G
2400–2800 m
Native (S Mexico)

[Lycianthes ciliolata var. pratorum Bitter]
Recorded from Honduras by Molina R. (1975)–probably a misidentification for *L. acapulcensis* as according to Ellen Dean *L. ciliolata* only goes to G.

Lycianthes connata J. L. Gentry
Phytologia 26: 271. 1973.
Shrub
Ch, G
2000–3000 m
Endemic

Lycianthes cuchumatanensis J. L. Gentry
Phytologia 26: 273. 1973.
Vine
Ch, G
1500–2600 m
Endemic

Lycianthes cuneata Standl. = **Witheringia cuneata** (Standl.) Hunz.

Lycianthes escuintlensis (J. M. Coult.) D'Arcy = **Lycianthes heteroclita** (Sendtn.) Bitter

Lycianthes furcatistellata Bitter
Die Gattung Lycianthes 403. 1919.
Shrub or vine
CR
1500–2700 m
Endemic
May be synonymous with *L. hygrophila* Bitter of Panama

Lycianthes geminiflora (M. Martens & Galeotti) Bitter
Die Gattung Lycianthes 497. 1919.
Solanum geminiflorum M. Martens & Galeotti
Shrub
Ch, G
1500–2000 m
Native (S Mexico)

Lycianthes gongylodes J. L. Gentry
Phytologia 26: 274. 1973.
Shrub
G
2600–3000 m
Endemic

Lycianthes gorgonea Bitter
Repert. Spec. Nov. Regni Veg. 20: 364. 1920.
Shrub
Ch, B, G
200–400 m
Endemic

Lycianthes grandifrons Bitter
Die Gattung Lycianthes 418. 1919.
Herb
CR, P
ca. 600 m
Endemic

Lycianthes guianense (Dunal) Bitter
Die Gattung Lycianthes 341. 1919.
Solanum guianense Dunal
Shrub or vine
P
0–1000(–2000) m
Native (South America)

Lycianthes hawkesiana D'Arcy
Ann. Missouri Bot. Gard. 60: 641. 1973 [1974].
Shrub
P
300–900 m
Endemic

Lycianthes heteroclita (Sendtn.) Bitter
Die Gattung Lycianthes 494. 1919.
Solanum heteroclitum Sendtn.
Herb, shrub, or tree
Ch, B, G, H, ES, N, CR, P
0–1500 m
Native (S Mexico)

Lycianthes hortulana Standl. & L. O. Williams
Ceiba 3: 58. 1952.
Shrub or vine
H
1000–2400 m
Endemic

Lycianthes howardiana D'Arcy
Ann. Missouri Bot. Gard. 60: 642. 1973 [1974].
Shrub or vine
P
ca. 1000 m
Endemic

Lycianthes hygrophila Bitter
Die Gattung Lycianthes 402. 1919.
Vine
P
2100–2300 m
Endemic
May be synonymous with *L. furcatistellata* Bitter of Costa Rica

Lycianthes hypoleuca Standl.
Trop. Woods 9: 12. 1927.
Shrub or vine
C, QR, B, G
100–700 m
Endemic

Lycianthes inaequalis C. V. Morton & Standl. = **Witheringia cuneata** (Standl.) Hunz.

Lycianthes inaequilatera (Rusby) Bitter
Die Gattung Lycianthes 439. 1919.
Bassovia inaequilatera Rusby
Shrub
N, CR, P
350–1400 m
Native (Andean South America)

Lycianthes inconspicua Bitter
Repert. Spec. Nov. Regni Veg. 20: 368. 1924.
Shrub
G
1300–1900 m
Endemic

Lycianthes laxissima Standl. = **Witheringia cuneata** (Standl.) Hunz.

Lycianthes lenta (Cav.) Bitter
Die Gattung Lycianthes 364. 1919.
Solanum lentum Cav.
Shrub or vine
Ch, B, G, H, ES, N, CR
0–1000 m
Native (Mexico, Cuba)

[Lycianthes limensis Standl. & L. O. Williams]
Recorded from Honduras by Molina R. (1975). Not a validly published name.

Lycianthes limitanea (Standl.) J. L. Gentry
Phytologia 26: 275. 1973.
Solanum limitaneum Standl.
Vine
Ch, B, G
500–1800 m
Endemic

Lycianthes luteynii D'Arcy
Ann. Missouri Bot. Gard. 60: 643. 1973 [1974].
Shrub or vine
P
ca. 1680 m
Endemic

Lycianthes maxonii Standl.
J. Wash. Acad. Sci. 17: 14. 1927.
Herb or shrub
N, CR, P
0–1800 m
Endemic

Lycianthes maxonii var. *appendiculata* Standl. = **Lycianthes maxonii** Standl.

Lycianthes maxonii var. *grandidentata* D'Arcy = **Lycianthes maxonii** Standl.

Lycianthes mitrata (Greenm.) Bitter = **Lycianthes heteroclita** (Sendtn.) Bitter

Lycianthes moziniana (Dunal) Bitter
Die Gattung Lycianthes 408. 1919.
Solanum mozinianum Dunal
Herb
Ch, G
ca. 2000 m
Native (Mexico)

Lycianthes multiflora Bitter
Die Gattung Lycianthes 361. 1919.
Shrub or vine
B, N, CR
0–1600 m
Endemic

Lycianthes multiflora var. *extustomentosa* Bitter = **Lycianthes multiflora** Bitter

Lycianthes multiflora var. *plicitomentosa* Bitter = **Lycianthes multiflora** Bitter

Lycianthes nitida Bitter
Die Gattung Lycianthes 501. 1919.
Epiphytic shrub or vine
Ch, B, G, H, N, CR
0–1200 m
Native (S Mexico, Ecuador)

Lycianthes ocellata (Donn. Sm.) C. V. Morton & Standl.
Field Mus. Nat. Hist., Bot. Ser. 22: 274. 1940.
Solanum sideroxyloides var. *ocellatum* Donn. Sm.
Shrub or vine
Ch, G, N
1000–1800 m
Endemic

Lycianthes orogenes Standl. & Steyerm.
Field Mus. Nat. Hist., Bot. Ser. 23: 229. 1947.
Shrub or treelet
Ch, G
1000–1800 m
Endemic

Lycianthes pilosissima (M. Martens & Galeotti) Bitter
Die Gattung Lycianthes 378. 1919.
Solanum pilosissimum M. Martens & Galeotti
Shrub
Ch, G, ES
1500–2000 m
Native (S Mexico)

Lycianthes porteriana D'Arcy
Ann. Missouri Bot. Gard. 60: 645. 1973 [1974].
Shrub or vine
CR, P
1300–2000 m
Native (Ecuador)

Lycianthes purpusii (Brandegee) Bitter
Die Gattung Lycianthes 382. 1919.
Solanum purpusii Brandegee
Shrub or vine
Ch, B, G, H
0–1000 m
Native (S Mexico)

Lycianthes quichensis (J. M. Coult. & Donn. Sm.) Bitter
Die Gattung Lycianthes 428. 1919.
Solanum quichense J. M. Coult. & Donn. Sm.
Shrub
Ch, G, H
2200–3900 m
Endemic

Lycianthes rantonnei (Carrière) Bitter
Die Gattung Lycianthes 332. 1919.
Solanum rantonnei Carrière
Shrub
G, H, ES
Middle elevations
Introduced and cultivated (S South America)

Lycianthes sanctaeclarae (Greenm.) D'Arcy
Ann. Missouri Bot. Gard. 63: 364. 1976 [1977].
Solanum sanctaeclarae Greenm.
Shrub or tree
N, CR, P
0–200 m
Endemic

Lycianthes sideroxyloides (Schltdl.) Bitter
Die Gattung Lycianthes 403. 1919.
Vine
Y, QR, B, H
ca. 100 m
Native (Mexico)

Lycianthes stephanocalyx (Brandegee) Bitter
Repert. Spec. Nov. Regni Veg. 18: 315. 1922.
Solanum stephanocalyx Brandegee
Herb or subshrub
Ch, B, G, H
0–200 m
Native (central & S Mexico)

Lycianthes synanthera (Sendtn.) Bitter
Die Gattung Lycianthes 499. 1919.
Solanum synantherum Sendtn.
Epiphytic shrub or treelet
Ch, B, G, H, N, CR, P
0–1000 m
Native (S Mexico, Ecuador, Peru)

Lycianthes tricolor (Sessé & Moç. ex Dunal) Bitter
Die Gattung Lycianthes 385. 1919.
Solanum tricolor Sessé & Moç. ex Dunal
Shrub or vine
Ch, G, H, ES
1800–2500 m
Native (S Mexico)

Lycianthes tysoniana D'Arcy
Ann. Missouri Bot. Gard. 60: 647. 1973 [1974].
Shrub or vine
P
ca. 750 m
Endemic

Lycianthes vulpina Standl. = **Lycianthes purpusii** (Brandegee) Bitter

Lycium L.

1 species

Lycium carolinianum Walt.
Fl. Carol. 84. 1788.
Shrub
Y
0 m
Native (SE U.S.A., Mexico)

Lycopersicon esculentum Mill. = **Solanum lycopersicum** L.

Lycopersicon esculentum var. *cerasiforme* (Dunal) A. Gray = **Solanum lycopersicum** L.

Margaranthus solanaceus Schltdl. = **Physalis solanaceus** (Schltdl.) Axelius

Markea Rich.

1 species; 1 endemic species

Markea campanulata (Donn. Sm.) Lundell = **Merinthopodium neuranthum** (Hemsl.) Donn. Sm.

Markea crosbiana D'Arcy = **Schultesianthus crosbiana** (D'Arcy) S. Knapp

Markea dressleri D'Arcy = **Merinthopodium neuranthum** (Hemsl.) Donn. Sm.

Markea internexa (S. F. Blake) Lundell = **Merinthopodium neuranthum** (Hemsl.) Donn. Sm.

Markea leucantha Donn. Sm. = **Schultesianthus leucanthus** (Donn. Sm.) Hunz.

[Markea megalandra (Dunal) D'Arcy]
Accepted name in D'Arcy (1973 [1974]) and Gentry & Standley (1974). Misapplied name for *Schultesianthus leucanthus* (Donn. Sm.) Hunz.

Markea neurantha Hemsl. = **Merinthopodium neuranthum** (Hemsl.) Donn. Sm.

Markea panamensis Standl.
J. Arnold Arbor. 11: 127. 1930.
Epiphytic shrub
P
0–800 m
Endemic

[Markea ulei (Damm.) Cuatrec.]
Accepted name in D'Arcy (1973 [1974]). Misapplied name for *Markea panamensis–M. ulei* is an Amazonian species.

Markea uniflora Lundell = **Schultesianthus uniflorus** (Lundell) S. Knapp

Markea venosa Standl. & C. V. Morton = **Schultesianthus venosus** (Standl. & C. V. Morton) S. Knapp

Melananthus Walp.

1 species

Melananthus guatemalensis (Benth. ex Hemsl.) Soler.
Ber. Deutsch. Bot. Ges. 9: 84. 1891.
Microschwenckia guatemalensis Benth. ex Hemsl.
Herb
Ch, B, G, H, N, CR
800–1500 m
Native (S Mexico, Cuba, Brazil)

Merinthopodium Donn. Sm.

1 species; 1 endemic species

Merinthopodium neuranthum (Hemsl.) Donn. Sm.
Bot. Gaz. 23: 12. 1897.
Markea neurantha Hemsl.
Epiphytic shrub
Ch, B, G, H, N, CR, P
0–2000 m
Endemic

Microschwenckia guatemalensis Benth. ex Hemsl. = **Melananthus guatemalensis** (Benth.) Soler.

Nicandra Adans.

1 species

Nicandra physalodes (L.) Gaertn.
Fruct. Sem. Pl. 2: 237. 1791.
Atropa physalodes L.
Herb or subshrub
Ch, G, H, ES, N, CR
600–1800 m
Introduced (native of Peru; E U.S.A., Mexico, South America to Argentina, West Indies)

Nicotiana L.

5 species

Nicotiana glauca Graham
Edinburgh New Philos. J. 5: 175. 1828.
Shrub or treelet
Ch, G, H, ES, P
0–2000 m
Introduced and cultivated (native of South America; naturalized in subtropics worldwide)

Nicotiana plumbaginifolia Viv.
Elench. Pl. 26, t. 5. 1802.
Herb
Ch, G, H
0–1500(2000) m
Native in Mexico and Guatemala; also introduced and cultivated (S U.S.A., South America, West Indies)

Nicotiana rustica L.
Sp. Pl. 180. 1753.
Herb
Y
0 m
Introduced and cultivated (native to the Andes)

Nicotiana×sanderae W. Watson
Fl. & Sylva 2: 216. 1904.
Herb
Ch
Altitude unknown
Introduced and cultivated (Brazil; widely cultivated)

Nicotiana tabacum L.
Sp. Pl. 180. 1753.
Herb or shrub
Ch, Y, QR, B, G, H, ES, N, CR, P
0–1300 m
Introduced and cultivated (native of the Andes)

Parascopolia acapulcensis Baill. = **Lycianthes acapulcensis** (Baill.) D'Arcy

Petunia Juss.

1 species

Petunia hybrida Hort. ex Vilm.
Fl. Pleine Terre 1: 615. 1863.
Herb or subshrub
Ch, Y, G, H, ES, P
0–500(–2000) m

Introduced and cultivated (horticultural hybrid between *P. integrifolia* (Hook.) Schinz & Thell. and *P. axillaris* (Lam.) Britton, Stern & Poggenb.)

Physalis L.

25 species; 4 endemic species

Physalis amica Standl. & Steyerm. = **Tzeltalia amphitricha** (Bitter) E. Estrada & M. Martínez

Physalis amphitricha (Bitter) Standl. & Steyerm. = **Tzeltalia amphitricha** (Bitter) E. Estrada & M. Martínez

Physalis angulata L.
Sp. Pl. 183. 1753.
Herb
Ch, Y, B, H, ES, N, CR, P
0–1600 m
Native (E to central U.S.A., Mexico, South America, West Indies, Old World tropics)

Physalis angustiphysa Waterf.
Rhodora 69: 228. 1967.
Herb
Ch, G
2500–2900 m
Native (Mexico)

Physalis arborescens L. = **Physalis campechiana** L.

Physalis calidaria Standl. & Steyerm. = **Tzeltalia calidaria** (Standl. & Steyerm.) E. Estrada & M. Martínez

Physalis campanula Standl. & Steyerm.
Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 18. 1943.
Herb
Ch, G
2200–2500 m
Native (S Mexico)

Physalis campechiana L.
Syst. Nat., ed. 10 2: 933. 1759.
Shrub
T, Ch, Y, C, QR, G
0–950 m
Native (Mexico)

Physalis carnosa Standl. & Steyerm. = **Physalis minuta** Griggs

Physalis chenopodifolia Lam.
Tabl. Encycl. 2:28. 1794.
Herb
Y
0 m
Introduced (Mexico)

Physalis chimalteca Standl. & Steyerm. = **Tzeltalia calidaria** (Standl. & Steyerm.) E. Estrada & M. Martínez

Physalis cinerascens (Dunal) Hitchc.
Key Spring Fl. Manhattan: 32. 1894.
Physalis pensylvanica var. *cinerascens* Dunal
Herb
Ch, C, Y
40–1170 m
0 m
Native (S U.S.A., E Mexico)

Physalis cordata Mill.
Gard. Dict. ed. 8, Physalis no. 14. 1768.
Herb
Ch, Y, C, G, H, ES, N, CR, P
0–1800 m
Native (S U.S.A., Mexico, South America, West Indies)

Physalis coztomatl Dunal
A. DC., Prodr. 13: 450. 1852.
Herb
Ch
2000–2700 m
Native (Mexico)

Physalis gracilis Miers
Ann. Mag. Nat. Hist. ser. 2, 4: 37. 1849.
Herb
T, Ch, Y, C, B, G, H, ES, N, CR, P
0–1600 m
Native (Mexico, N South America)

Physalis hirsuta Dunal = **Physalis pubescens** L.

Physalis hylophila Standl. = **Physalis pubescens** L.

Physalis ignota Britton
Mem. Torrey Bot. Club 16: 100. 1920.

Herb
Ch, G, H, ES, N, CR, P
0–900 m
Native (West Indies, Ecuador)

Physalis ingrata Standl.
Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 391. 1938.
Herb
H
ca. 1200 m
Endemic

Physalis ixocarpa Brot. ex Hornem.
Hort. Bot. Hafn. Suppl. 26. 1819.
Herb
T, Ch, N, CR
40–1450 m
Native (Mexico)

Physalis lagascae Roem. & Schult.
Syst. Veg. 4: 679. 1819.
Herb
T, Ch, Y, C, QR, G, H, ES, N, CR, P
0–1500 m
Native (U.S.A., Mexico, Ecuador, Martinique, Cuba (introduced))

Physalis lagascae var. *glabrescens* O. E. Schulz = **Physalis lagascae** Roem. & Schult.

Physalis lassa Standl. & Steyerm.
Field Mus. Nat. Hist., Bot. Ser. 23: 19. 1943.
Herb
Ch, G
200–2000 m
Endemic

Physalis leptophylla B. L. Rob. & Greenm.
Proc. Amer. Acad. Arts 29: 389. 1894.
Herb
G, H, N, CR
110–600 m
Native (Mexico)

Physalis maxima Mill. = **Physalis pruinosa** L.

Physalis mayana Standl. = **Physalis campechiana** L.

Physalis melanocystis (B. L. Rob.) Bitter
Repert. Spec. Nov. Regni Veg. 20: 369. 1924.
Withania melanocystis B. L. Rob.
Shrub
Ch, QR, G, H
200–400 m
Native (Mexico)

Physalis micrantha Link = **Physalis lagascae** Roem. & Schult.

Physalis microcarpa Urb. & Ekman
Ark. Bot. 21A(5): 59. 1927.
Herb
Ch, G, H, ES, N
0–1900 m
Native (West Indies)

Physalis minuta Griggs
Torreya 3: 138. 1903.
Herb
Ch, H, N, CR, P
0–900 m
Native (Mexico)

[Physalis mollis Nutt.]
Accepted name in Reyes-García & Sousa (1997), but a misidentification for *P. cinerascens* (Dunal) Hitchc.

Physalis nicandroides Schltdl.
Linnaea 19: 311. 1846.
Herb
Ch, Y, G, H, N, CR
100–1800 m
Native (S Mexico, Paraguay)

Physalis nicandroides var. *attenuata* Waterf. = **Physalis pruinosa** L.

Physalis parviculea S. F. Blake
Contr. U.S. Natl. Herb. 24: 20. 1922.
Herb
G, ES
0 m
Endemic

Physalis parviflora Lag., non R. Br. = **Physalis lagascae** Roem. & Schult.

Physalis pensylvanica var. *cinerascens* Dunal = **Physalis cinerascens** (Dunal) Hitchc.

Physalis pentagona S. F. Blake = **Physalis ignota** Britton

Physalis philadelphica Lam.
Encycl. 2: 101. 1786.
Herb
Ch, QR, B, G, ES, N CR, P
0–2460 m
Native and cultivated (Mexico, West Indies; introduced in U.S.A.)

Physalis philadelphica var. *parviflora* Waterf. = **Physalis philadelphica** Lam.

Physalis porphyrophysa Donn. Sm. = **Physalis melanocystis** (B. L. Rob.) Bitter

Physalis porrecta Waterf.
Rhodora 69: 237. 1967.
Herb
Ch, G, N, CR, P
1500–2500 m
Endemic

[Physalis pringlei Greenm.]
This record from Breedlove (1986) is a misidentification of a specimen of *Physalis coztomatl* Dunal.

Physalis pruinosa L.
Sp. Pl. 184. 1753.
Herb
Ch, Y, G, H, ES, N, CR
0–2000 m
Native (Mexico, South America)

Physalis pubescens L.
Sp. Pl. 183. 1753.
Herb, subshrub, or shrub
T, Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–1000(–1500) m
Native (U.S.A., Mexico, South America, West Indies)

Physalis pubescens var. *hygrophila* (Mart.) Dunal = **Physalis pubescens** L.

Physalis solanaceus (Schltdl.) Axelius
Phytologia 79: 11. 1995.
Herb
Y, Ch, G, H, CR
10–1300 m
Native (SW U.S.A., Mexico)

[Physalis sordida Fernald]
Recorded from Honduras by Molina R. (1975), but probably misidentified as only cited from Mexico in Estrada & Martínez (1999).

Physalis turbinata Medik. = **Physalis pubescens** L.

Physalis viscosa var. *yucatanensis* Waterf. = **P. cinerascens** (Dunal) Hitchc.

Pionandra allophylla Miers = **Solanum allophyllum** (Miers) Standl.

Plowmania Hunz. & Subils

1 species; 1 endemic species

Plowmania nyctaginoides (Standl.) Hunz. & Subils
Kurtziana 18: 127. 1986.
Brunfelsia nyctaginoides Standl.
Subshrub
Ch, G
1000–3800 m
Endemic

Rahowardiana wardiana D'Arcy = **Juanulloa wardiana** (D'Arcy) S. Knapp

Saracha confinis C. V. Morton = **Jaltomata confinis** (C. V. Morton) J. L. Gentry

Saracha procumbens var. *repandidentata* Dunal = **Jaltomata repandidentata** (Dunal) Hunz.

Saracha solanacea (L'Hér.) Miers = **Witheringia solanacea** L'Hér.

[Saracha umbellata Don]
Accepted name in Standley & Calderón (1941), but misapplied–probably for *Jaltomata procumbens* (Cav.) J. L. Gentry. *Saracha umbellata* is a South American species.

Saracha viscosa Schrad. = **Leucophysalis viscosa** (Schrad.) Hunz.

Schultesianthus Hunz.

4 species; 3 endemic species

Schultesianthus crosbiana (D'Arcy) S. Knapp
Novon 5: 283. 1995.
Markea crosbiana D'Arcy
Shrub
P
1500–1800 m
Endemic

Schultesianthus leucanthus (Donn. Sm.) Hunz.
Kurtziana 10: 35. 1977.
Markea leucantha Donn. Sm.
Shrub
Ch, G, H, CR, P
1400–1800 m
Native (northern South America)

[Schultesianthus megalandrus (Hemsl.) Hunz.]
Recorded from Costa Rica by Haber (1991), but misapplied for *Schultesianthus leucanthus* (Donn. Sm.) Hunz.

Schultesianthus uniflorus (Lundell) S. Knapp
Novon 5: 283. 1995.
Markea uniflora Lundell
Epiphytic shrub
Ch, G
2000–3000 m
Endemic

Schultesianthus venosus (Standl. & C. V. Morton) S. Knapp
Novon 5: 283. 1995.
Markea venosa Standl. & C. V. Morton
Epiphytic shrub
CR, P
1500–2000 m
Endemic

Schwenckia Vahl

2 species

Schwenckia americana L.
Gen. Pl. ed. 6: 577. 1764.
Herb
Ch, Y, QR, B, G, H, ES, N, CR, P
0–1500 m
Native (S Mexico, South America, Cuba, Africa)

Schwenkia lateriflora (Vahl) Carvalho
Loefgrenia 37: 2. 1969.
Chaetochilus lateriflorus Vahl
Herb or subshrub
N, CR
100–400 m
Native? (Brazil, Venezuela)

Sicklera solanacea (L'Hér.) Sendtn. = **Witheringia solanacea** L'Hér.

Sicklera tentandra A. Braun & Bouché = **Witheringia solanacea** L'Hér.

Solandra Sw.

5 species; 2 endemic species

Solandra brachycalyx Kuntze
Revis. Gen. Pl. 2: 453. 1891.
Epiphytic shrub
G, N, CR, P
1200–2100 m
Endemic
Record from G is possibly a misidentification of *S. nizandensis*, as Bernardello & Hunziker (1987) did not record *S. brachycalyx* from there.

Solandra grandiflora Sw.
Kongl. Vetensk. Acad. Handl. 8: 300, t. 11. 1787.
Epiphytic shrub or vine
P
600–1000 m
Native and cultivated (S Mexico, West Indies)
Name often misapplied. According to Bernardello & Hunziker (1987), this species occurs only in Panama and only as cultivated plants. However, recorded by others from Ch, B, G, H, ES & CR.

Solandra longiflora Tussac
Fl. Antill. 2: 49, pl. 12. 1818.
Vine
B
0 m

Cultivated (native to N South America and West Indies)

Solandra maxima (Sessé & Moç.) P. S. Green
Bot. Mag. 176: t. 506. 1967.
Datura maxima Sessé & Moç.
Shrub or vine
Ch, G, H, N, CR, P
0–2000 m
Native and cultivated (Mexico, Colombia, Venezuela)

Solandra nizandensis Matuda
Anales Inst. Biol. Univ. Nac. México 43: 60. 1972 [1974].
Epiphytic shrub
Ch, B, G, H, ES
2100–2500 m
Endemic

Solanum L.

115 species; 23 endemic species

Solanum accrescens Standl. & C. V. Morton
Publ. Field. Mus. Nat. Hist., Bot. Ser. 18: 1075. 1938.
Shrub or treelet
N, CR, P
300–900 m
Endemic

Solanum acerifolium Dunal
Solan. Syn. 41. 1816.
Herb or shrub
Ch, G, H, N, CR, P
1000–2000 m
Native (S Mexico, N South America, NE Brazil)

[Solanum acerosum Sendtn.]
Accepted name in D'Arcy (1973), but misapplied for *Solanum acerifolium* Dunal.

Solanum acidochondrum Bitter = **Lycianthes acidochondra** (Bitter) Bitter

[Solanum aculeatissimum Jacq.]
Accepted name in Breedlove (1986) and recorded from Honduras by Nelson (1978), but the name has been misapplied for a number of species in section *Acanthophora*.

Solanum aculeolatum M. Martens & Galeotti
Bull. Acad. Roy. Sci. Bruxelles 12: 143. 1845.
Vine
G, H
300–1500 m
Native (S Mexico)

Solanum adhaerens Roem. & Schult.
Syst. Veg. 4: 669. 1819.
Vine
C, B, H, ES, N, CR, P
500–1300 m
Native (Mexico, N South America)

Solanum adscendens Sendtn.
Fl. Bras. 10: 17, t. 1, f. 9–12. 1846.
Herb
Ch, G, H, ES, N, CR
0–1800 m
Native (S Mexico, South America)

Solanum agrimoniifolium Rydb.
Bull. Torrey Bot. Club 51: 154. 1924.
Herb
Ch, G, H
1900–3400 m
Native (S Mexico)

Solanum aligerum Schltdl.
Linnaea 19: 301. 1845.
Shrub or tree
Ch, G, H, ES, CR
2400–3100 m
Native (S Mexico, Andean South America to Bolivia and Argentina)

Solanum allophyllum (Miers) Standl.
J. Wash. Acad. Sci. 17: 16. 1927.
Pionandra allophylla Miers
Herb
N, CR, P
0–900 m
Native (N South America)

Solanum amatitlanense J. M. Coult. & Donn. Sm. = **Lycianthes amatitlanensis** (J. M. Coult. & Donn. Sm.) Bitter

Solanum amazonicum Ker Gawl. = **Solanum tridynamum** Dunal

Solanum americanum Mill.
Gard. Dict. ed. 8, Solanum no. 5. 1768.
Herb or subshrub
T, Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–3100 m
Native (W U.S.A., Mexico, South America, West Indies, Old World tropics)

[Solanum anceps Ruiz & Pav.]
Accepted name in D'Arcy (1973 [1974]), but misapplied for *Solanum dimorphandrum* S. Knapp.

Solanum angustifolium Mill.
Gard. Dict. ed. 8, Solanum no. 15. 1768.
Herb
Ch, Y, H
900–1500 m
Native (Mexico)

Solanum antillarum O. E. Schulz = **Solanum nudum** Dunal

Solanum aphyodendron S. Knapp
Ann. Missouri Bot. Gard. 72: 564. 1985.
Shrub or tree
Ch, G, H, ES, N, CR, P
700–1600 m
Native (Mexico, South America S to Bolivia along Andes)

Solanum appendiculatum Dunal
Solan. Syn. 5. 1816.
Vine
Ch, G, H, ES, N
1300–3800 m
Native (S-central Mexico)

Solanum arboreum Dunal
Solan. Syn. 20. 1816.
Shrub or tree
N, CR, P
0–2100 m
Native (Mexico, South America)

[Solanum argenteum Dunal ex Poir.]
Misapplied name for *S. lepidotum* Dunal; *S. argenteum* occurs only in Brazil.

Solanum armentalis J. L. Gentry & D'Arcy
Ann. Missouri Bot. Gard. 64: 376. 1977 [1978].
Shrub
CR
ca. 1070 m
Endemic

Solanum arrazolense J. M. Coult. & Donn. Sm. = **Lycianthes arrazolensis** (J. M. Coult. & Donn. Sm.) Bitter

Solanum asperum Rich.
Actes Soc. Hist. Nat. Paris 1: 107. 1792.
Treelet or tree
B, H, CR, P
0–800 m
Native (Trinidad, S to Brazil)

Solanum atitlanum K. E. Roe
Brittonia 19: 364. 1967.
Shrub or treelet
QR, G, H, N
(60)600–2000 m
Endemic

Solanum aturense Dunal
Solan. Syn. 32. 1816.
Shrub, tree, or vine
B, H, N, CR, P
0–800 m
Native (S Mexico, N South America)

Solanum betaceum Cav.
Anales Hist. Nat. 1: 44. 1799.
Treelet
Ch, G, H, CR
600–1800(–3200) m
Introduced and cultivated (native of South America)

[Solanum bicolor Willd. ex Roem. & Shult.]
Accepted name in Standley (1930), Molina R. (1975), Standley & Calderón (1941), and Sousa S. & Cabrera C. (1983), but misapplied, possibly for *S. erianthum* D. Don or *S. hazenii* Britton.

Solanum blodgettii Chapm. = **Solanum donianum** Walp.

Solanum boquetense Standl. = **Solanum candidum** Lindl.

Solanum brenesii C. V. Morton & Standl. = **Solanum rovirosanum** Donn. Sm.

Solanum brevipedicellatum K. E. Roe
Brittonia 19: 361. 1967.
Shrub or treelet
Ch, G
1500–1800 m
Native (S Mexico)

Solanum bulbocastanum Dunal
in Poir., Encycl. 3: 749. 1814.
Herb
Ch, G
1300–2300 m
Native (Mexico, N South America)

Solanum bulbocastanum var. *glabrum* Correll = **Solanum bulbocastanum** Dunal

Solanum bulbocastanum var. *partitum* Correll = **Solanum bulbocastanum** Dunal

Solanum campechiense L.
Sp. Pl. 187. 1753.
Herb or shrub
Ch, Y, B, G, H, ES, CR
0–400 m
Native (Mexico, N South America, West Indies)

Solanum candidum Lindl.
Edward's Bot. Reg. 25(misc.): 73. 1839.
Herb or shrub
Ch, Y, B, G, H, ES, N, CR, P
0–1100 m
Native (Mexico, Ecuador, Peru, Venezuela)

Solanum canense Rydb.
Bull. Torrey Bot. Club 51: 174. 1924.
Herb or vine
G, H, ES, N, CR, P
0–1000 m
Native (W Venezuela and Colombia to Ecuador)

Solanum capsicoides All.
Mélanges Philos. Math. Soc. Roy. Turin 5: 64. 1773.
Herb or subshrub
B, H, ES, N, CR
0–1100 m
Introduced (native to Brazil, introduced worldwide)

Solanum caripense Dunal
Solan. Syn. 8. 1816.
Herb or vine
H, N, CR, P
1200–2300 m
Native (Mexico, N South America)

Solanum cervantesii Lag. = **Solanum pubigerum** Dunal

Solanum cervantesii subsp. *glabrum* (Dunal) C. V. Morton = **Solanum pubigerum** Dunal

Solanum chiapasense K. E. Roe
Brittonia 19: 367. 1967.
Shrub or treelet
Ch, QR, G, N
1000–2100 m
Endemic

Solanum chiapense Brandegee = **Lycianthes chiapensis** (Brandegee) Standl.

Solanum chloropetalon Schltdl. = **Solanum myriacanthum** Dunal

Solanum chrysotrichum Schltdl.
Linnaea 19: 304. 1846.
Subshrub, shrub, treelet, or tree
Ch, G, H, N, CR, P
1000–2500 m
Native (S Mexico)

Solanum ciliolatum M. Martens & Galeotti = **Lycianthes ciliolata** (M. Martens & Galeotti) Bitter

Solanum circinatum Bohs
Taxon 44: 585. 1995.
Shrub, treelet, or tree
Ch, G, H, N, CR, P
0–1300 m
Native (S Mexico, South America)

Solanum clarum Correll
Contr. Texas Res. Found., Bot. Stud. 1:10,t.4.1950.
Herb
Ch, G
3100–3800 m
Endemic

Solanum cobanense J. L. Gentry
Phytologia 26: 276. 1973.
Vine
Ch, G, N
900–2600 m
Endemic

Solanum coibae Riley = **Solanum leucocarpon** Dunal

Solanum connatum Correll = **Solanum appendiculatum** Dunal

Solanum cordovense Sessé & Moç.
Fl. Mexic. ed. 2: 51. 1894.
Shrub or tree
Ch, B, G, H, N, CR, P
200–1500 m
Native (S Mexico)

Solanum cornutum Lam. = **Solanum angustifolium** Mill.

Solanum darienense S. Knapp
Ann. Missouri Bot. Gard. 73: 738. 1986 [1987].
Shrub
P
500–1000 m
Native (Colombia)

Solanum dasyanthum Brandegee
Univ. Calif. Publ. Bot. 6: 193. 1915.
Shrub
Y, G, H, N
0–900 m
Native (S Mexico)

Solanum dasyneuron S. Knapp
Ann. Missouri Bot. Gard. 72: 563. 1985.
Shrub or treelet
Ch, G
2500–3000 m
Endemic

Solanum deflexum Greenm. = **Solanum adscendens** Sendtn.

Solanum demissum Lindl.
J. Roy. Hort. Soc. 3: 69, 70. 1848.
Herb
Ch, G
2200–3700 m
Native (S-central Mexico)

Solanum diaboli Standl. & L. O. Williams = **Solanum dasyanthum** Brandegee

Solanum dimorphandrum S. Knapp
Bull. Nat. Hist. Mus. London, Bot. 30: 21. 2000.
Herb or subshrub
P
800–1000 m
Native (N South America)

Solanum diphyllum L.
Sp. Pl. 184. 1753.
Shrub
Ch, C, QR, B, G, H, ES, N, CR
0–300 m
Native (S Mexico)

Solanum diversifolium Dunal
Solan. Syn. 8. 1816.
Shrub or treelet
CR, P
0–400 m
Native (Colombia, Venezuela)

Solanum donianum Walp.
Repert. Bot. Syst. 3: 54. 1844.
Shrub
Y, C, QR, B, G
0 m
Native (S Florida, S Mexico, Bahamas)

Solanum donnell-smithii J. M. Coult. = **Solanum adhaerens** Roem. & Schult.

Solanum dotanum C. V. Morton = **Solanum aligerum** Schltdl.

Solanum dulcamaroides Dunal
in Poir., Encycl. 3: 751. 1814.
Shrub or vine
Ch, G, N
1100–3200 m
Native (S Mexico)

Solanum edwardsii Standl. = **Solanum cordovense** Sessé & Moç.

Solanum elaeagnifolium Cav.
Icon. 3: 22, t. 243, p. 115. 1794.

Subshrub
T?, Ch
0 m
Introduced? (SW U.S.A., S Mexico, Argentina)

Solanum erianthum D. Don
Prodr. Fl. Nepal. 96. 1825.
Shrub, treelet, or tree
Ch, Y, C, QR, B, G, H, N, CR, P
0–2000 m
Native (S U.S.A., Mexico, West Indies, Galapagos Islands; adventive in Old World)

Solanum erythrotrichum Fernald
Proc. Amer. Acad. Arts 35: 561. 1900.
Shrub or treelet
B, G, H, CR, P
500–1900 m
Native (N South America, Venezuela, Guayana)

Solanum eshbaughianum D'Arcy = **Solanum leucocarpon** Dunal

Solanum evolvulifolium Greenm.
Bot. Gaz. 37: 211. 1904.
Epiphytic shrub or vine
CR, P
1800–2100 m
Native (Colombia, Ecuador)

Solanum extensum Bitter = **Solanum cordovense** Sessé & Moç.

Solanum ferrugineum Jacq.
Pl. Hort. Schoenbr. 3: 46, t. 334. 1798.
Shrub
Ch, ES?
1000–1200 m
Native (Mexico)

Solanum flavescens Dunal = **Solanum hirtum** Vahl

Solanum fontium Standl. & Steyerm. = **Solanum narcoticosmum** Bitter

Solanum fortunense Bohs
Taxon 44: 584. 1995.
Treelet
CR, P
900–1800 m
Endemic

Solanum fosbergianum D'Arcy
Ann. Missouri Bot. Gard. 60: 700. 1973 [1974].
Treelet
P
900–1200 m
Endemic

Solanum fraxinifolium Dunal
in DC., Prodr. 13(1): 39. 1852.
Herb or vine
G, N, CR, P
2000–2600 m
Native (Colombia, Venezuela)

Solanum geminiflorum M. Martens & Galeotti = **Lycianthes geminiflora** (M. Martens & Galeotti) Bitter

Solanum glaucescens Zucc.
Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2: 325. 1831–1836.
Shrub or vine
Ch
ca. 1500 m
Native (S Mexico)

Solanum globiferum Dunal = **Solanum myriacanthum** Dunal

Solanum granelianum D'Arcy = **Solanum pensile** Sendtn.

Solanum grossularia Bitter = **Solanum fraxinifolium** Dunal

Solanum guanicense Urb. = **Solanum campechiense** L.

Solanum guianense Dunal = **Lycianthes guianense** (Dunal) Bitter

Solanum hamatile Brandegee = **Solanum glaucescens** Zucc.

Solanum hartwegii Benth. = **Solanum lanceolatum** Cav.

Solanum hayesii Fernald
Proc. Amer. Acad. Arts 35: 560. 1900.
Shrub or tree
N, CR, P
0–1000 m
Native (Colombia)

Solanum hazenii Britton
Bull. Torrey Bot. Club 48: 338. 1922.
Shrub or tree
G, H, N, CR, P
0–850 m
Native (W Mexico, N South America, West Indies)

[Solanum hernandesii Dunal]
Accepted name in Standley & Calderón (1941) and recorded from Honduras by Molina R. (1975). The name is of uncertain application–could be *S. chrysotrichum* Schltdl. or *S. lanceolatum* Cav.

Solanum heteroclitum Sendtn. = **Lycianthes heteroclita** (Sendtn.) Bitter

Solanum hirsutissimum Standl. = **Solanum pectinatum** Dunal

[Solanum hirsutum Vahl]
Recorded from Honduras by Molina R. (1975), but probably a misprint for *S. hirtum* Vahl.

Solanum hirtum Vahl
Symb. Bot. 2: 40. 1791.
Herb, subshrub, treelet, or tree
Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–700(–1200) m
Native (Mexico, West Indies, N South America)

[Solanum hispidum Pers.]
Accepted name in D'Arcy (1973 [1974]), Gentry & Standley (1974), and Molina R. (1975), but misapplied for *Solanum chrysotrichum* Schltdl.

Solanum houstonii Dunal = **Solanum tampicense** Dunal

Solanum huehuetecum Standl. & Steyerm. = **Solanum lignescens** Fernald

Solanum huitlanum Brandegee = **Solanum candidum** Lindl.

Solanum imberbe Bitter
Repert. Spec. Nov. Regni Veg. 18: 62. 1922.
Shrub
CR, P
0–100 m
Native (South America (Colombia, Venezuela, Ecuador), Trinidad)

Solanum incomptum Bitter
Repert. Spec. Nov. Regni Veg. 18: 60. 1922.
Shrub or treelet
CR, P
1600–2100 m
Endemic

Solanum inscendens Rydb. = **Solanum appendiculatum** Dunal

[Solanum intermedium Sendtn.]
Accepted name in D'Arcy (1973 [1974]), but misapplied to specimens of *Solanum imberbe* Bitter.

Solanum ipomoea Sendtn. = **Solanum pensile** Sendtn.

Solanum jamaicense Mill.
Gard. Dict. ed. 8, Solanum no. 17. 1768.
Herb or shrub
Ch, B, G, H, N, CR, P
0–1000 m
Native (S Mexico, West Indies, South America)

[Solanum juglandifolium var. oerstedii Bitter]
This variety of the widespread South American *S. juglandifolium* Dunal is known only from the type. *Solanum juglandifolium* Dunal is not otherwise known from Mesoamerica, and this record from CR (as "America centralis?" in the protologue; Repert. Spec. Nov. Regni Veg. 11: 461. 1912) is certainly due to a label misprint or confusion (I. Peralta, pers. comm.).

Solanum lanceifolium Jacq.
Collectanea 2: 286. 1789.
Vine
Ch, Y, C, QR, B, G, H, N, CR, P
0–1800 m
Native (S Mexico, N South America, West Indies)

Solanum lanceolatum Cav.
Icon. 3: 23, t. 245. 1795.
Shrub or tree
Ch, B, G, H, ES, N, CR, P
700–3200 m
Native (Mexico)

[Solanum laurifolium L. f.]
Accepted name in Standley & Calderón (1941: 195) and Breedlove (1986), but misapplied for *Solanum lanceolatum* Cav.

Solanum lentum Cav. = **Lycianthes lenta** (Cav.) Bitter

Solanum lepidocaule Standl. & L. O. Williams = **Solanum ramonense** C. V. Morton & Standl.

Solanum lepidotum Dunal
Solan. Syst. 17. 1816.
Shrub or treelet
B, G, H, ES, N, CR, P
100–1000 m
Native (S Mexico, N South America)

Solanum leucocarpon Dunal
in Poir., Encycl. 3: 756. 1814.
Shrub or tree
P
0–100 m
Native (South America (Colombia, Venezuela, Guayanas, Ecuador, Peru, Bolivia, Brazil))

Solanum lignescens Fernald
Proc. Amer. Acad. Arts 33: 91. 1897.
Herb or shrub
Ch, G, H, N
1000–1300 m
Native (Mexico)

Solanum limitaneum Standl. = **Lycianthes limitanea** (Standl.) J. L. Gentry

Solanum longiconicum Bitter = **Solanum oxycarpum** Schiede

Solanum lundellii Standl. = **Solanum cordovense** Sessé & Moç.

Solanum lycopersicum L.
Sp. Pl. 185. 1753.
Herb or subshrub
Ch, Y, QR, B, G, H, ES, N, CR, P
0–2500 m
Introduced and cultivated (native of South America; worldwide)

Solanum macrantherum Dunal = **Solanum dulcamaroides** Dunal

Solanum macrotonum Bitter
Repert. Spec. Nov. Regni Veg. 11: 222. 1912.
Herb or subshrub
CR, P
1900–3000 m
Native (Ecuador, Colombia, Peru, Venezuela (Andean))

Solanum madrense Fernald = **Solanum ferrugineum** Jacq.

Solanum mammosum L.
Sp. Pl. 187. 1753.
Herb or subshrub
Ch, Y, B, G, H, ES, N, CR, P
0–1500 m
Introduced and cultivated (S Mexico, South America, West Indies)

Solanum martinsii Van Heurck & Müll. Arg.
Observ. Bot. 73. 1870.
Shrub
CR
ca. 600 m
Native (N South America, Brazil)

Solanum melongena L.
Sp. Pl. 186. 1753.
Herb or shrub
Y, B, G, H, ES, N, P
ca. 100 m
Introduced and cultivated (native of Asia)

Solanum microleprodes Bitter
Repert. Spec. Nov. Regni Veg. 13: 96. 1913.
Shrub or tree
P
0–600 m
Native (Colombia, Venezuela)

Solanum microleprodes var. *felicis* D'Arcy = **Solanum microleprodes** Bitter

Solanum mirabile Standl. & C. V. Morton = **Solanum aturense** Dunal

Solanum mitlense Dunal
in DC., Prodr. 13(1): 314. 1852.
Shrub or small tree
Ch
Altitude unknown (1400–2000 m in Mexico)
Native (Mexico)
Breedlove (1986) recorded this species from Chiapas. We have seen no specimens, and it may be based on a misidentification of a robust plant of *S. lanceolatum* (Nee, pers. comm.).

Solanum mitratum Greenm. = **Lycianthes heteroclita** (Sendtn.) Bitter

Solanum molinarum J. L. Gentry = **Solanum aculeolatum** M. Martens & Galeotti

Solanum morelliforme Bitter & Münch
Repert. Spec. Nov. Regni Veg. 12: 154, t. 2. 1913.
Epiphytic herb
Ch, G
1600–2800 m
Native (E-central Mexico)

Solanum mozinianum Dunal = **Lycianthes moziniana** (Dunal) Bitter

Solanum muenscheri Standl. & Steyerm.
Field Mus. Nat. Hist., Bot. Ser. 22: 275. 1940.
Shrub
G
2500–3500 m
Endemic

Solanum muricatum Aiton
Hort. Kew. 1: 250. 1789.
Subshrub or shrub
G, H, ES, CR, P
1000–2700 m
Introduced and cultivated (native to Andean region)

Solanum myriacanthum Dunal
Hist. Nat. Solanum 218, t. 19. 1813.
Herb or subshrub
Ch, B, G, H, ES, N, CR
600–1600 m
Native (S Mexico)

Solanum narcoticosmum Bitter
Repert. Spec. Nov. Regni Veg. 18: 55. 1922.
Shrub
Ch, G
2100–2800 m
Endemic

Solanum nigrescens M. Martens & Galeotti
Bull. Acad. Roy. Sci. Bruxelles 12: 140. 1845.
Herb, subshrub, or shrub
Ch, G, H, ES, N, CR, P
800–3900 m
Native (S U.S.A. to Bolivia)

Solanum nigricans M. Martens & Galeotti
Bull. Acad. Roy. Sci. Bruxelles 12: 134. 1845.
Shrub or treelet
Ch, G, H
1200–2700 m
Native (S Mexico)

[Solanum nigrum L.]
Accepted name in Standley (1930), Standley & Calderón (1941), and Sousa S. & Cabrera C. (1983), but an Old World species and the name misapplied for *Solanum americanum* Mill. and/or *S. nigrescens* M. Martens & Galeotti.

Solanum nudum Dunal
Solan. Syn. 20. 1816.
Shrub, treelet, or tree
T, Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–2800 m
Native (S Mexico, South America, Antilles)

Solanum oaxacanum Dunal = **Solanum glaucescens** Zucc.

Solanum ochraceo-ferrugineum (Dunal) Fernald = **Solanum rudepannum** Dunal

Solanum olivaeforme Donn. Sm. = **Solanum phaseoloides** Polak.

Solanum oxycarpum Schiede
in Schltdl., Hort. Hal. 1: 5, t. 3. 1841.
Herb

G, H, CR, P
1800–3000 m
Native and cultivated (S Mexico)

[Solanum palmilloe Hemsl.]
?*Solanum palmillae* Standl. Accepted name in Reyes-García & Sousa S. (1997); *S. palmillae* occurs only in Veracruz, not in Chiapas.

Solanum panamense Van Heurck & Müll. Arg. = **Witheringia solanacea** L'Hér.

Solanum pastillum S. Knapp
Ann. Missouri Bot. Gard. 72: 558. 1985.
Shrub
N, CR
500–1400 m
Endemic

Solanum pavonii Dunal = **Solanum lanceifolium** Jacq.

Solanum peckii S. F. Blake = **Witheringia solanacea** L'Hér.

Solanum pectinatum Dunal
in DC., Prodr. 13(1): 250. 1852.
Shrub
CR, P
100–600 m
Native (S Mexico, N South America)

Solanum pensile Sendtn.
in Mart., Fl. Bras. 10: 50. 1846.
Shrub or vine
CR, P
0–400(3000) m
Native (Venezuela, Colombia, Ecuador, Brazil, Guayanas, Bolivia)

Solanum perattenuatum I. M. Johnst. = **Solanum cordovense** Sessé & Moç.

Solanum pertenue Standl. & C. V. Morton
Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1089. 1938.
Shrub
N, CR
ca. 700 m
Endemic

Solanum phaseoloides Polak.
Linnaea 41: 585. 1877.
Herb
Ch, B, G, ES, CR, P
300–1700 m
Native (N South America)

Solanum pilosissimum M. Martens & Galeotti = **Lycianthes pilosissima** (M. Martens & Galeotti) Bitter

Solanum pittieri Bitter = **Solanum trizygum** Bitter

Solanum pseudocapsicum L.
Sp. Pl. 184. 1753.
Subshrub or shrub
Ch, G, P
ca. 1830 m
Possibly native in Chiapas; also introduced and cultivated (Mexico to South America; widely cultivated)

Solanum pubigerum Dunal
Hist. Nat. Solanum 160, t. 6. 1813.
Shrub or treelet
Ch, G, H, ES
2000–3200 m
Native (S Mexico)

Solanum pulverulentifolium K. E. Roe
Brittonia 19(4): 365. 1967.
Treelet or tree
Ch
ca. 1550 m
Endemic

Solanum purpusii Brandegee = **Lycianthes purpusii** (Brandegee) Bitter

Solanum quichense J. M. Coult. & J. D. Smith = **Lycianthes quichensis** (J. M. Coult. & Donn. Sm.) Bitter

Solanum quinquangulare Willd. ex Roem. & Schult. = **Solanum acerifolium** Dunal

Solanum quitoense Lam.
Tabl. Encycl. 2: 16, no. 2326. 1794.
Herb, subshrub, or shrub
H, N, CR, P
900–1700 m
Introduced and cultivated (Ecuador, Colombia)

Solanum ramonense C. V. Morton & Standl.
Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1090. 1938.
Shrub
CR, P
700–2400 m
Endemic

Solanum rantonnei Carrière = **Lycianthes rantonnei** (Carrière) Bitter

[Solanum rantonnetii Carrière ex Lesc.]
Misspelling for *Solanum rantonnei* Carrière = *Lycianthes rantonnei.*

Solanum roblense Bitter
Repert. Spec. Nov. Regni Veg. 18: 62. 1922.
Shrub
CR
100–2800 m
Endemic

Solanum roei Ugent & Iltis = **Solanum cordovense** Sessé & Moç.

Solanum rojasianum (Standl. & Steyerm.) Bohs
Taxon 44: 586. 1995.
Cyphomandra rojasiana Standl. & Steyerm.
Shrub
Ch, B, G, H
1000–1500 m
Endemic

Solanum rovirosanum Donn. Sm.
Bot. Gaz. 48: 297. 1909.
Shrub or treelet
T, Ch, B, G, N, CR, P
0–1500 m
Native (S Mexico)

Solanum rubidum Standl. & C. V. Morton = **Solanum martinsii** Van Heurck & Müll. Arg.

Solanum rudepannum Dunal
in DC., Prodr. 13(1): 264. 1852.
Shrub, treelet, or tree
Ch, B, G, ES, N, CR, P
0–2500 m
Native (Mexico, Colombia, Ecuador)

Solanum rugosum Dunal
in DC., Prodr. 13(1): 108. 1852.
Shrub or treelet
Ch, B, G, H, N, CR, P
0–1800 m
Native (South America S to Brazil, West Indies)

Solanum salsum Standl. = **Solanum dasyanthum** Brandegee

Solanum sanctaeclarae Greenm. = **Lycianthes sanctaeclarae** (Greenm.) D'Arcy

[Solanum salviifolium Lam.]
Accepted name in Standley & Calderón (1941), but misapplied for *Solanum lepidotum*.

Solanum scandens Mill.
Gard. Dict., ed. 8, Solanum 19. 1768.
Vine or shrub
T, Ch, QR
0–100 m
Native (Mexico)
M. Nee (in litt., and on herbarium sheets) indicates this species should be transferred to *Lycianthes*.

Solanum schlechtendalianum Walp.
Repert. Bot. Syst. 3: 61. 1844.
Shrub or tree
Ch, B, G, H, ES, N, CR, P
0–1600 m
Native (S Mexico, South America, Cuba)

Solanum seaforthianum Andrews
Bot. Repos. 8: t. 504. 1808.
Vine
Ch, Y, B, G, H, ES, N, CR, P
0–1700 m
Introduced and cultivated (probably native to the West Indies; widely cultivated)

Solanum sessiliflorum Dunal
in Poir., Encycl. 3: 775. 1814.
Herb or shrub
N, CR, P
0–100 m
Introduced and cultivated (Ecuador, Peru, Brazil)

Solanum setosum (Brandegee) Bitter = **Solanum adscendens** Sendtn.

Solanum sideroxyloides var. *ocellatum* Donn. Sm. = **Lycianthes ocellata** (Donn. Sm.) C. V. Morton & Standl.

Solanum siparunoides Ewan = **Solanum aturense** Dunal

Solanum skutchii Correll
Contr. Texas Res. Found., Bot. Stud. 1: 4, t. 1. 1950.
Vine
G, N
900–2800 m
Native (Mexico)

[Solanum somniculentum Kuntze]
Accepted name in Standley & Calderón (1941), but a misdetermination for *Lycianthes* sp., probably *L. acapulcensis* (Baill.) D'Arcy.

Solanum stellatiglandulosum Bitter
Repert. Spec. Nov. Regni Veg. 16: 389. 1920.
Shrub
CR, P
1400–1600 m
Native (Colombia)

Solanum stephanocalyx Brandegee = **Lycianthes stephanocalyx** (Brandegee) Bitter

Solanum steyermarkii Carvalho
Ann. Missouri Bot. Gard. 78: 243. 1991.
Tree
Ch, G, H, CR, P
1200–2000 m
Native (Venezuela, Ecuador, Peru)

Solanum storkii C. V. Morton & Standl.
Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1093. 1938.
Shrub or tree
CR, P
2700–3100 m
Endemic

Solanum stramoniifolium Jacq.
Misc. Austriac. 2: 298. 1781.
Shrub
N, P
0–100 m
Native (N South America)

Solanum suaveolens Kunth & C. D. Bouché
Index Sem. (Berlin) 1848: 14. 1848.
Herb, subshrub, or vine
Ch, B, G, H, ES, CR
Below 1000 m
Native (S-central Mexico, N South America (to Bolivia))

Solanum subinerme Jacq.
Enum. Syst. Pl. 15. 1760.
Shrub
P
300–900 m
Native (South America, Antilles)

Solanum synantherum Sendtn. = **Lycianthes synanthera** (Sendtn.) Bitter

Solanum tacanense Lundell = **Solanum appendiculatum** Dunal

Solanum taeniotrichum Correll
Contr. Texas Res. Found., Bot. Stud. 1: 6, f. 2. 1950.
Herb or vine
CR
3000–3300(3400) m
Endemic

Solanum tampicense Dunal
in DC., Prodr. 13(1): 284. 1852.
Vine
Ch, B, G, H, ES
0–100 m
Native (U.S.A. (Florida), S Mexico, West Indies)

Solanum tequilense A. Gray = **Solanum candidum** Lindl.

Solanum torvum Sw.
Prodr. 47. 1788.
Shrub or tree
Ch, Y, C, QR, B, G, H, ES, N, CR, P
0–1500 m
Native (Mexico, South America; West Indies; introduced to Old World tropics)

Solanum tricolor Sessé & Moç. ex Dunal = **Lycianthes tricolor** (Sessé & Moç. ex Dunal) Bitter

Solanum tridynamum Dunal
in Poir., Encycl. 3: 776. 1814.
Subshrub or shrub
Y, QR
0–100 m
Native (Mexico)

Solanum trizygum Bitter
Repert. Spec. Nov. Regni Veg. 11: 470. 1912.
Herb
Ch, G, H, CR, P
100–2100 m
Native (Mexico, Venezuela)

Solanum tuberosum L.
Sp. Pl. 185. 1753.
Herb
Ch, Y, G, H, ES, N, CR, P
800–1000 m
Introduced and cultivated (native of South America)

Solanum tuerckheimii Greenm.
in Donn. Sm., Bot. Gaz. 37: 212. 1904.
Shrub
QR, B, G, N, CR
200–1600 m
Endemic

Solanum umbellatum Mill.
Gard. Dict. ed. 8, Solanum no. 27. 1768.
Shrub, treelet, or tree
Ch, Y, B, G, H, ES, N, CR, P
0–2100 m
Native (Mexico, N South America; West Indies; introduced into Africa)

Solanum unguis-cati Standl. = **Solanum wendlandii** Hook. f.

Solanum vacciniiflorum Standl. & L. O. Williams
Ceiba 1: 247. 1951.
Shrub or treelet
CR, P
1900–2700 m
Endemic

Solanum valerianum C. V. Morton & Standl.
Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1097. 1938.
Shrub
N, CR, P
0–200 m
Endemic

Solanum verapazense Standl. & Steyerm. = **Solanum dasyanthum** Brandegee

Solanum verbascifolium L. = **Solanum donianum** Walp.
Rejected name

Solanum vernale Standl. & L. O. Williams = **Solanum cordovense** Sessé & Moç.

Solanum wendlandii Hook.f.
Bot. Mag. 113: t. 6914. 1887.
Shrub or vine
Ch, G, H, ES, N, CR, P
200–2800 m
Native and also cultivated (S Mexico)

Solanum woodsonii Correll
Wrightia 2: 137. 1961.
Herb
P
3100–4000 m
Native (Venezuela)

Solanum wrightii Benth.
Fl. Hongk. 243. 1861.
Tree
H, N, CR
0–1200 m
Introduced and cultivated (native to Bolivia; widely cultivated in tropical countries)

Solanum yucatanum Standl. = **Solanum dasyanthum** Brandegee

Streptosolen Miers

1 species

Streptosolen jamesonii (Benth.) Miers
Ann. Mag. Nat. Hist. ser. 2, 5: 209. 1850.
Browallia jamesonii Benth.
Shrub

ES, CR, P
1000–1500 m
Introduced and cultivated (native to Ecuador and Colombia; widely cultivated)

Tzeltalia E. Estrada & M. Martínez

2 species; 2 endemic species

Tzeltalia amphitricha (Bitter) E. Estrada & M. Martínez
Brittonia 50: 291. 1998.
Physalis amphitricha Bitter
Herb
Ch, B, G
1300–2700 m
Endemic

Tzeltalia calidaria (Standl. & Steyerm.) E. Estrada & M. Martínez
Brittonia 50: 292. 1998.
Physalis calidaria Standl. & Steyerm.
Herb
Ch, G
2300–2900 m
Endemic

Withania melanocystis B. L. Rob. = **Physalis melanocystis** (B. L. Rob.) Bitter

Witheringia L'Hér.

13 species; 7 endemic species

Witheringia affinis (C. V. Morton) Hunz. = **Brachistus nelsonii** (Fernald) D'Arcy

Witheringia asterotricha (Standl.) Hunz.
Kurtziana 5: 151. 1969.
Capsicum asterotrichum Standl.
Herb or shrub
CR, P
600–1700 m
Endemic

Witheringia bristaniana D'Arcy = **Acnistus arborescens** (L.) Schltdl.

Witheringia coccoloboides (Dammer) Hunz.
Kurtziana 5: 132. 1969.
Acnistus coccoloboides Dammer
Herb or shrub
Ch, B, N, CR, P
300–2500 m
Native (Colombia, Ecuador)

Witheringia correana D'Arcy
Ann. Missouri Bot. Gard. 60: 766. 1973 [1974].
Herb
N, CR, P
200–300 m
Endemic

Witheringia cuneata (Standl.) Hunz.
Kurtziana 5: 118. 1969.
Lycianthes cuneata Standl.
Herb or shrub
Ch, G, N, CR, P
0–1900 m
Native (S Mexico, N South America)

Witheringia exiguiflora D'Arcy = **Cuatresia exiguiflora** (D'Arcy) Hunz.

Witheringia folliculoides D'Arcy & J. L. Gentry
Ann. Missouri Bot. Gard. 74: 453. 1987.
Shrub or treelet
CR
0–300 m
Endemic
This species is probably a member of *Cuatresia*, but the formal transfer has not yet been made.

Witheringia fournieri Van Heurck & Müll. Arg. = **Brachistus stramoniifolius** (Kunth) Miers

Witheringia fuscoviolacea (Cufod.) Hunz. = **Witheringia coccoloboides** (Dammer) Hunz.

Witheringia hunzikeri D'Arcy
Ann. Missouri Bot. Gard. 60: 768. 1973 [1974].
Shrub
P
100–400 m
Native (Colombia, Chocó)
This species is probably a member of *Brachistus*, but the formal transfer has not yet been made.

Witheringia laxissima (Standl.) D'Arcy = **Witheringia cuneata** (Standl.) Hunz.

Witheringia macrantha (Standl. & C. V. Morton) Hunz.
Kurtziana 5: 114. 1969.
Shrub
CR, P
900–1500 m
Endemic

Witheringia macrophylla Kunth ex Dunal = **Witheringia solanacea** L'Hér.

Witheringia maculata (C. V. Morton & Standl.) Hunz.
Kurtziana 5: 117. 1969.
Capsicum maculatum C. V. Morton & Standl.
Herb
CR, P
1600–2000 m
Endemic

Witheringia meiantha (Donn. Sm.) Hunz.
Kurtziana 5: 147. 1969.
Brachistus meianthus Donn. Sm.
Herb or shrub
Ch, G, H, N, CR, P
300–1700 m
Native (S Mexico)

Witheringia mexicana (B. L. Rob.) Hunz.
Kurtziana 5: 131. 1969.
Bassovia mexicana B. L. Rob.
Shrub, treelet
CH
1000–1600 m
Native (Mexico)

Witheringia morii D'Arcy
Ann. Missouri Bot. Gard. 63: 368. 1976 [1977].
Shrub
CR, P
100–1200(–2000) m
Endemic
This species is probably a member of *Cuatresia*, but the formal transfer has not yet been made.

Witheringia mortonii Hunz.
Kurtziana 5: 123. 1969.
Shrub
CR
200–1400 m
Endemic

Witheringia nelsonii (Fernald) Hunz. = **Brachistus nelsonii** (Fernald) D'Arcy

Witheringia physocalycia (Donn. Sm.) J. L. Gentry = **Cuatresia riparia** (Kunth) Hunz.

Witheringia pogonandra Lem. = **Witheringia solanacea** L'Hér.

Witheringia rhomboidea Dunal = **Capsicum rhomboideum** (Dunal) Kuntze

Witheringia riparia Kunth = **Cuatresia riparia** (Kunth) Hunz.

Witheringia silvigaudens (Standl. & L. O. Williams) Hunz. = **Witheringia meiantha** (Donn. Sm.) Hunz.

Witheringia solanacea L'Hér. var. *silvigaudens* (Standl. & L. O. Williams) Hunz. = **Witheringia meiantha** (Donn. Sm.) Hunz.

Witheringia solanacea L'Hér.
Sert. Angl. 1: 33, t. 1. 1788.
Herb, subshrub, shrub, or treelet
T, Ch, B, G, H, CR, P
0–2440 m
Native (S Mexico, South America, West Indies)

Witheringia solanacea var. *asterotricha* (Standl.) Hunz. = **Witheringia asterotricha** (Standl.) Hunz.
Combination at subspecific level never validly made

Witheringia solanacea var. *solanacea* = **Witheringia solanacea** L'Hér.

Witheringia stramoniifolia Kunth = **Brachistus stramoniifolius** (Kunth) Miers

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6

JALTOMATA (SOLANACEAE) OF COSTA RICA

Thomas Mione and Leon Yacher

ABSTRACT. Three species of *Jaltomata* (Solanaceae) are recognized based on comparative morphology, including principal components analysis of morphological characteristics. *Jaltomata procumbens* grows from 1000 to 2900 m in Costa Rica and is distinguished by its straight filaments, anthers of uniform size, and straight styles. *Jaltomata repandidentata* grows from 400 to 1200 m, is characterized by its sigmoid filaments, anther size variation within the flower, and curved styles, and is reported from Central America for the first time. *Jaltomata darcyana* is a new species of the seasonally dry Pacific Coast, found from 0 to 320 m; it has straight filaments, anther size variation within the flower, and curved styles. The former two species are protogynous: anther dehiscence occurs the day after the flower opens. *Jaltomata darcyana*, however, lacks a pistillate phase and is functionally hermaphroditic when the flower opens. The first chromosome count for *J. darcyana* is reported: $2n = 24$. A key to the *Jaltomata* of Costa Rica is included.

RESUMEN. Tres especies de *Jaltomata* (Solanaceae) son reconocidas basándose en morfología comparada, incluyendo análisis de componentes principales (PCA) de caracteres morfológicos. *Jaltomata procumbens* es una especie que crece comúnmente entre los 1000–2900 m en Costa Rica y se distingue por presentar filamentos rectos, anteras de tamaño uniforme y estilos rectos. *Jaltomata repandidentata* es una especie que crece comúnmente entre los 400–1200 m; se caracteriza por tener filamentos sigmoides, anteras de tamaño variable dentro de la misma flor, estilos curvados, y se reporta por la primera vez para América Central. Se describe *Jaltomata darcyana*, una nueva especie de la región de la costa estacionalmente seca del Pacífico de Costa Rica; tiene filamentos rectos, anteras de tamaño variable en cada flor, estilos curvados, y crece entre 0–320 m. Las dos primeras especies son protóginas: la dehiscencia de las anteras ocurre un día después la apertura de la flor. Por otro lado, *J. darcyana* no tiene una fase pistilada y es funcionalmente hermafrodita al abrirse la flor. Se reporta por primera vez el número de cromosomas de *J. darcyana*: $2n = 24$. Se incluye una clave para el género *Jaltomata* en Costa Rica.

Key words: Costa Rica, epiphyte, *Jaltomata*, Solanaceae.

This study is part of ongoing research on the systematics of *Jaltomata* Schltdl. (Mione et al., 1993, 1994, 2000a, 2000b; Mione & Bye, 1996). The genus *Jaltomata* includes two groups: (a) an herbaceous lineage having rotate corollas and black (rarely green) fruits, distributed from Arizona, U.S.A., to Bolivia, and (b) a woody lineage having campanulate, tubular, and rotate corollas and orange to red fruits, with its center of diversity in the Andes but with one species each in the Greater Antilles and the Galápagos Islands. This study was conceived in the early 1990s when T.M. realized that the *Flora of Costa Rica* (Standley, 1937) listed only a single species of *Jaltomata*, but herbarium specimens from the country exhibited more morphological and ecological variation than is normally present in one species.

The combination of attributes that distinguish *Jaltomata* from other Solanaceae genera is: simple leaves, distinct peduncles, umbellate inflorescences, accrescent calyces that spread over the berry but never enclose it nor completely hide it in side view, filaments expanded at base, longitudinal anther dehiscence, and an ovarian nectar disk. Additional features present in (but not limited to) Costa Rica are: herbaceous habit, angular stems, a rotate corolla, microscopic glands (having unicellular stalks and multicellular heads) on the abaxial faces of the perianth, yellow anthers, clear nectar, and purple to black berries.

Prior to this study only a single species of *Jaltomata* was recognized in Costa Rica, though the genus grows from sea level to 2900 m elevation, from low-altitude seasonally dry forests to high-altitude consistently wet forests.

MATERIALS AND METHODS

Fieldwork in Costa Rica was done by T.M. in 1994, and by T.M. and L.Y. in 1995 and 2000. In the field plants were pressed, flowers were placed in 70% ethanol, leaves were desiccated for later DNA extraction, and habitat and locality data were recorded. Accessions from throughout the range of the genus have been grown in Connecticut for study since 1990.

Principal components analysis (PCA) is a widely used multivariate technique that can reveal hidden groupings (Quicke, 1993) and allows one to consider a mixture of uncorrelated and correlated variables (Goodman, 1974). The principal components are new, uncorrelated variables each of which is a linear combination of the original variables (Kleinbaum et al., 1988). PCA was performed on the correlation matrix using Minitab (1995), with each collection representing an OTU. Some collections studied in the living condition (Table 1) were not used in the PCA because of missing data. The characters used for PCA are listed in Table 2. The collections used for PCA are listed in Table 3, where means are based on 2 to 20 observations. Until now all *Jaltomata* of Costa Rica were considered a single species, *J. procumbens* (Cav.) J. L. Gentry, and so for comparison we included *J. grandiflora* (B. L. Rob. & Greenm.) D'Arcy, Mione & Davis, a morphologically distinct species from Mexico. Measurements were made with a dissecting microscope on living, pressed, and alcohol-preserved specimens.

Trichomes are not gland-tipped unless indicated as such. Finger hairs are uniseriate, unbranched, and multicellular. Branchlet hairs have multiple termini (Seithe, 1979). Gland-tipped finger hairs (on the *Jaltomata* of Costa Rica found only on the adaxial face of the corolla) have an expanded terminal cell that stains densely with neutral red. As well, the multicellular head of the stalked glands (common on the abaxial faces of the perianth) also stains densely with neutral red. Pollen grain diameter was measured after staining pollen 30 minutes in "cotton blue" stain; anthers were stored in 70% ethanol prior to staining. Floral phenology was observed in the field, and on healthy plants grown for study both outdoors and indoors under lights. Pollen grains were counted using the method of Anderson and Symon (1989). The ovule count of one locule was doubled to obtain the total ovules per ovary. Chromosomes were counted with the method of Bernardello and Anderson (1990); to obtain root tips seeds were sown on wet filter paper in a petri dish at room temperature under ambient light.

RESULTS

The first principal component accounts for 34.8% of the total variance (eigenvalue 6.27 divided by the sum of the eigenvalues, the latter the same as the number of original variables, 18). The second principal component has variance 2.84 and explains an additional 15.8% of the total variance. A plot of principal components one and two is presented as Figure 1. The third principal component has variance 2.5 and explains another 13.9% of the total variance. The first three components explain 64.5% of the variation; the first seven principal components explain 91% of the variation. The first principal component shows the highest loadings (Table 2) for characters that are among the most valuable for diagnosing species (see also key), e.g., characters: 9—filaments straight versus sigmoid, 11—the presence or absence of anther size variation within the flower, and 14—style straight versus curved. This is not surprising because the first component is the linear combination of the original variables that "best discriminates (produces the maximum distance) between individuals of a sample" (Pimentel, 1979). In a strict consensus tree (Mione, unpublished) based on DNA sequences (nuclear ribosomal DNA internal transcribed spacers 1 and 2 and the 5.8S gene), the collections of *J. repandidentata* form a monophyletic group. As well, the collections of *J. procumbens* of Costa Rica form a monophyletic group. *Jaltomata darcyana*, represented only by *Mione & Yacher 694*, does not group with any other Costa Rican collection(s) but instead groups with an accession from Mexico, outside of both the *J. procumbens* and *J. repandidentata* clades.

TAXONOMIC TREATMENT

Jaltomata Schltdl., Index Sem. (Halle) 1838: 8. 1838. TYPE: *Jaltomata edulis* Schltdl.

A clear explanation of the nomenclatural history of *Jaltomata* was presented by Gentry (1973).

In Costa Rica the following three species occur:

(1) *Jaltomata darcyana* Mione, described below

(2) *Jaltomata procumbens* (Cav.) J. L. Gentry

(3) *Jaltomata repandidentata* (Dunal) Hunz.

Jaltomata procumbens has straight filaments (Fig. 2C), anthers of uniform size that, in Costa Rica, are usually mucronate (Fig. 3F), and straight styles. This species grows from 1000 to 2900 m elevation. Plants grow to 2 m high in the upper part of this altitudinal range (field observations and herbarium specimen labels). *Jaltomata repandidentata*, on the other hand, has sigmoid filaments (Figs. 2E, 3A), anthers varying in size within the flower (Fig. 2D), and curved styles (Fig. 2D, E). This species grows from 400 to 1200 m elevation; plants grow to 1 m high. Flowers of these two species are protogynous, with filament elongation and anther dehiscence occurring on the second day the flower is open. In contrast, the collection made on the seasonally dry Pacific Coast, on the Nicoya Peninsula (*Mione & Yacher 694*), is distinct and is characterized by straight filaments, anthers of unequal size (when mature but undehisced), curved styles, absence of a pistillate phase, and is here designated a new species.

Jaltomata darcyana Mione, sp. nov. TYPE: Costa Rica. Nicoya Peninsula, Curú, 9°46′50″N, 84°56′05″W, 98 m, edge of pasture, 11 Jan. 2000, *T. Mione & L. Yacher 694* (holotype, NY!; isotypes, CONN!, CR!, MO!). Figures 2A, B, 3C, D.

Herba, caulibus insigniter angulatis, foliis ad 30 cm longis, inflorescentiis floribus 23 ut maxime, calyce aequabiliter viridi, corolla rotata, filamenta recta, antheris non mucronulatis, stylo curvo dirigente stigma ad latus, floribus numquam non hermaphroditis.

Erect glabrous herb to 1 m (described as 1.5 m on *Janzen 12125*) high. Stems hollow, green to purple, strongly angulate with 4 or 5 raised longitudinal ridges (Fig. 2A), to 2.5 cm diam. at base. Leaves alternate, often geminate, the blade elliptic, somewhat coriaceous, the faces

TABLE 1. Living *Jaltomata* collections studied.

Species	Country	Locality and elevation	Collector & #, and accession number, where applicable	Herbaria	Seen in the field	Grown for study in U.S.A.
J. darcyana	Costa Rica	Nicoya Peninsula, Curú, 98 m	*Mione & Yacher 694* (holotype)	CONN, CR, MO, NY	x	x
J. grandiflora	Mexico	Michoacán, Patzcuaro area, 2073 m	*Davis 1114*, Mione accession 454	COLO, CONN, F, MEXU, MO		x
J. procumbens	Costa Rica	Copey, 1740 m	*Sawyer 623*, Mione accession 395	INB		x
J. procumbens	Costa Rica	Border of Puntarenas and Alajuela, Cordillera de Tilarán, Monteverde Cloud Forest Reserve (on the Continental Divide at "La Ventana"), 1560 m	*Mione 583*	INB, MO	x	x
J. procumbens	Costa Rica	same as *583*	*Mione & L. Coe 606*	INB, NY	x	x
J. procumbens	Costa Rica	Parque Nacional Tapantí, 1420 m	*Mione & Yacher 684*	CONN	x	
J. procumbens	Costa Rica	Parque Nacional Tapantí, 1418 m	*Mione & Yacher 685*	CONN	x	
J. procumbens	Costa Rica	Parque Nacional Tapantí, 1744 m	*Mione & Yacher 686*	CONN	x	
J. procumbens	Costa Rica	Parque Nacional Tapantí, 1744 m	*Mione & Yacher 687*	CONN	x	
J. procumbens	Costa Rica	Parque Nacional Tapantí, 1763 m	*Mione & Yacher 688*	CONN	x	
J. procumbens	Costa Rica	Copey, 1740 m	*Mione & Yacher 689*	CONN	x	
J. procumbens	Costa Rica	Santa Maria, 1905 m	*Mione & Yacher 690*	CONN	x	
J. procumbens	Costa Rica	Estación Cuericí, 2600 m	*Mione & Yacher 692*	CONN	x	
J. procumbens	Costa Rica	Volcán Turrialba, 2700 m	*Mione & Yacher 693*	CONN	x	
J. procumbens	Costa Rica	Monteverde, 1500 m	*Mione & Haber 697*	CONN	x	
J. procumbens	Costa Rica	Monteverde, 1500 m	*Mione & Haber 698*	CONN	x	
J. procumbens	Costa Rica	Zarcero, 1650 m	*Mione et al. 699*	CONN	x	
J. procumbens	Costa Rica	Escazu, 1410 m	*Mione & Yacher 700*	CONN	x	
J. procumbens	Costa Rica	Río La Paz Pequeña, 1375 m	*Bohs seed 95-4*, Mione accession 635	CONN		x

J. procumbens	Costa Rica	Catarata San Luis, 1180 m	*Bohs seed 96-49*, Mione accession 636	INB		x
J. procumbens	Guatemala	Chiquimula, 1930 m	*Spooner et al. 7038*, Mione accession 321	AGUAT, BIGUA		x
J. procumbens	Mexico	Morelos, mpio. Tetela del Volcán, 2200 m	*Bye & Linares 10219*, Mione accession 456	MEXU		x
J. procumbens	Mexico	Mexico, rd. from Rt. 130 (134) to Valle de Bravo, 2600 m	*Mione 593*	CONN	x	x
J. procumbens	Mexico	Chiapas, Tzabalhó, 1650 m	*Eber s.n.*, Mione accession 401	CONN		x
J. procumbens	Mexico	Puebla, San Miguel Tenextatiloyan, 2500 m	*Mione 586*	CONN	x	x
J. procumbens	Mexico	Morelos, mpio. Tepoztlan, 1 km W of La Pera on Hwy. 95D, at rest stop, 2230 m	*Mione & Bye 599*	CONN	x	x
J. procumbens	Mexico	México, Valle de Bravo, rd. from 130 (134) to Valle de Bravo, 2500 m	*Mione & Basurto 596*	CONN	x	x
J. repandidentata	Bolivia	La Paz, Nor Yungas, 4.5 km below Yalosa then 13.7 km W on road up Río Huarinilla, 1200 m	*Mione et al. 565*	CONN, NY	x	x
J. repandidentata	Costa Rica	Puntarenas: Cordillera de Tilarán, along rd. from Carretera Interamericana to Monteverde, 700 m	*Mione & Yacher 605*	INB, NY, UT	x	x
J. repandidentata	Costa Rica	San Isidro, 580 m	*Mione & Yacher 691*	UT	x	
J. repandidentata	Costa Rica	Santa Elena, 1180 m	*Mione & Haber 696*	UT	x	
J. repandidentata	Mexico	Guerrero, 58 km from Atoyac de Alvarez on rd. to Puerto de Gallo, 1021 m	*Davis 822,* Mione accession 362	CONN, MO		x
J. repandidentata	Mexico	Veracruz, along old rd. 150 between Orizaba and Fortin; shade of coffee bushes, 1097 m	*Dean 266*, Mione accession 571	XAL		x
J. repandidentata	Nicaragua	Granada, Volcán Mombacho, common erect weed in coffee plantation, 450 m	*Mione & Coe 555*	CONN, HNMH, NY	x	x

TABLE 2.
Characters used in principal components analysis and component loadings (eigenvectors) on the first three components.

	Character	PC1	PC2	PC3
1	Altitude of collection locality	-0.286	-0.290	-0.061
2	Leaf margin: ranked from entire [0] to highly toothed [1]	0.122	-0.017	-0.107
3	Leaf vestiture of adaxial face: ranked from glabrous [0] to densely pubescent [1]	-0.169	-0.179	-0.402
4	Mean peduncle length maximum	-0.039	0.247	0.018
5	Flower: not protogynous [0], protogynous [1]	-0.110	-0.220	-0.115
6	Mean calyx diameter during anthesis	0.208	-0.222	0.350
7	Sepals reflexed during hermaphroditic phase: no [0], somewhat [1], strongly [2]	-0.024	-0.414	0.238
8	Number of corolla lobes: 5 lobes and no lobules [0], both 5 lobes and 5 lobules [1]	-0.096	-0.001	-0.521
9	Filaments: straight [0], sigmoid [1]	0.345	0.024	-0.064
10	Mean filament (including expanded base) length when fully elongated	0.288	-0.209	-0.208
11	Anther size variation within flower: absent [0], present [1]	0.368	0.141	0.006
12	Mean anther length (undehisced, living and/or preserved in 70% ethanol)	0.264	-0.356	-0.041
13	Anthers: lacking mucro [0], mucronate or mucronulate [1]	-0.217	0.278	0.256
14	Style: straight [0], curved [1]	0.368	0.141	0.006
15	Stigma: no groove [0], shallow groove [1], bilobed [2]	0.275	0.140	0.110
16	Mean style length (living and/or preserved in 70% ethanol)	0.274	-0.309	-0.215
17	Mean stigma diameter	-0.087	-0.373	0.430
18	Mean % of the filament (incl. expanded base) that bears hairs, proximal to distal	-0.246	-0.109	-0.034

TABLE 3.

Data used in principal components analysis: collection numbers are as in Table 1 and characters are numbered as in Table 2; darc, *Jaltomata darcyana;* gran, *J. grandiflora;* proc, *J. procumbens;* repa, *J. repandidentata.*

Species	Character Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
darc	**694**	98	0	0	27	0	12.5	0	0	0	4.4	1	1.9	0	1	1	4.2	0.5	12
gran	**454**	2073	1	1	15	1	17.0	1	0	0	4.4	0	3.0	0	0	0	5.2	1.1	50
proc	**321**	1930	1	1	52	1	8.3	0	1	0	6.2	0	1.9	0	0	0	5.4	0.3	55
proc	**401**	1650	1	1	62	1	11.5	0	0	0	5.1	0	2.8	0	0	0	5.0	0.5	15
proc	**456**	2200	0	1	29	1	7.0	0	1	0	4.9	0	1.9	0	0	0	4.0	0.5	30
proc	**583**	1560	0.2	0	70	1	12.3	0	0	0	4.1	0	1.6	1	0	1	3.1	0.6	29.8
proc	**586**	2500	0	0.1	27	1	11.1	0	0	0	6.1	0	2.4	0	0	0	4.9	0.8	15
proc	**593**	2600	0	1	30	1	8.1	0	1	0	4.6	0	2.0	0	0	1	3.8	0.4	37
proc	**596**	2500	0	0	34	1	10.6	1	0	0	5.1	0	2.0	0	0	1	4.1	1.0	24
proc	**599**	2230	0	0	43	1	17.0	0	0	0	6.5	0	2.8	0	0	1	4.9	0.6	15
proc	**635**	1375	0.6	0	75	1	12.0	0	0	0	3.4	0	1.8	1	0	1	3.0	0.7	27.3
proc	**636**	1180	1	1	25	1	10.9	0	0	0	4.2	0	1.6	0	0	0	3.5	0.7	60
proc	**689**	1740	1	1	50	1	9.1	0	0	0	3.3	0	1.7	1	0	0	3.6	0.6	42.5
proc	**692**	2600	0	1	31	1	10.3	0	0	0	5.7	0	1.8	1	0	0	4.9	0.7	47
proc	**693**	2700	0	0.2	35	1	14.5	0	0	0	4.4	0	1.5	1	0	0	3.5	0.7	88
proc	**699**	1650	0.7	0.2	28	1	10.3	0	0	0	3.6	0	1.7	1	0	0	2.9	0.6	30
proc	**700**	1410	0.7	0.3	27	1	8.6	0	0	0	3.3	0	1.7	1	0	0	2.8	0.6	20
repa	**555**	450	1	0.1	35	1	13.1	0	0	1	6.9	1	2.6	0	1	2	5.4	0.5	15
repa	**605**	700	1	0	33	1	14.6	0	0	1	6.8	1	2.7	0	1	1	6.1	0.5	15
repa	**691**	580	1	0.3	37	1	14.5	0	0	1	7.2	1	2.6	0	1	1	5.2	0.6	10

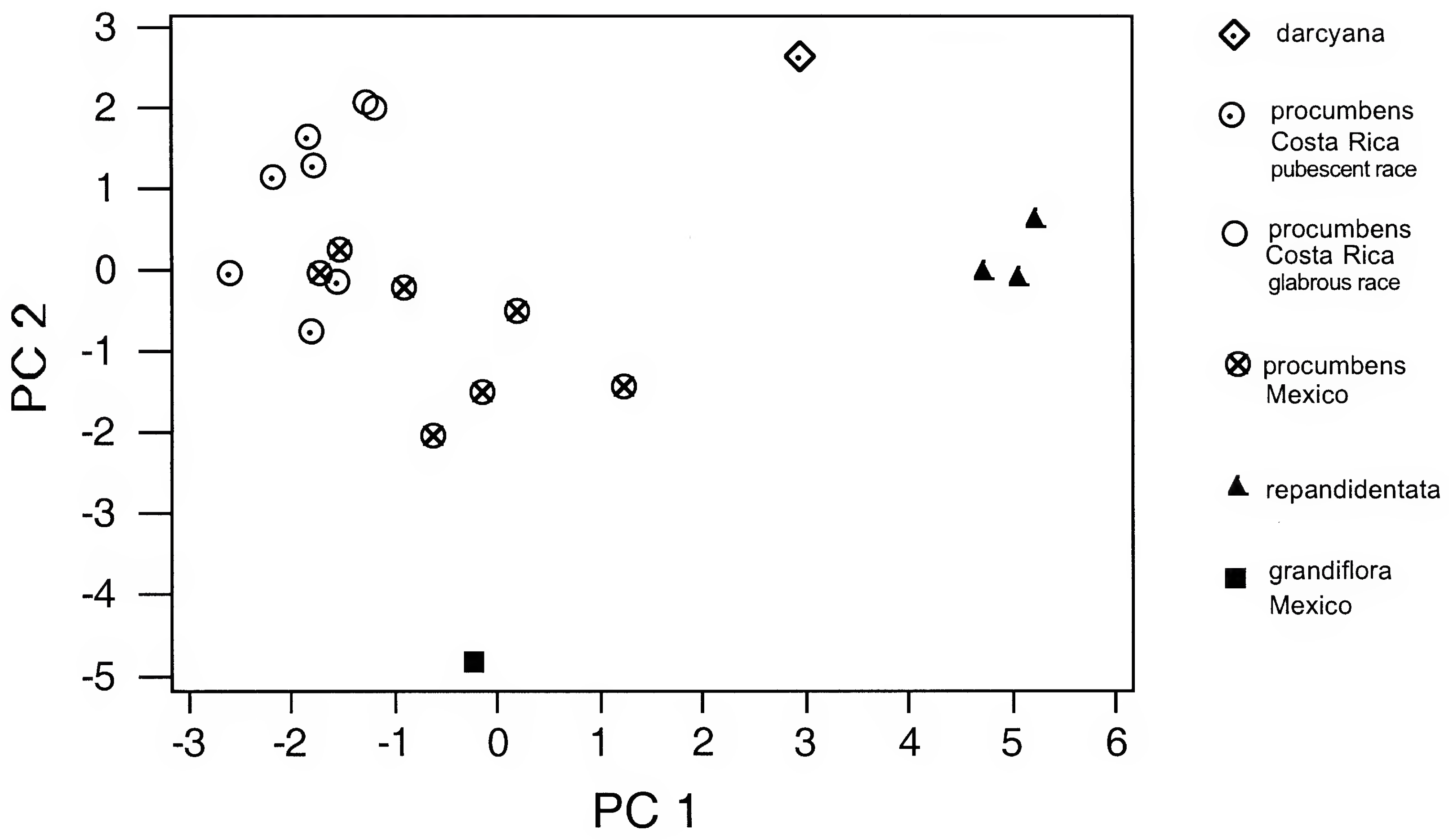

Figure 1. Plot of principal components one and two using 18 morphological characteristics. Each plotted point represents a collection listed in Table 3.

glabrous and lustrous, to 30 cm long, the length to width ratio 1.5–1.8, the proximal 13%–16% of the blade cuneate, the tip usually acuminate (Fig. 2A), the margin entire or nearly so and on smaller, younger leaves sparsely ciliolate with finger hairs to 0.1 mm long; petiole to 2.5 cm long. Inflorescence axillary or arising from a stem dichotomy, umbellate, to 23-flowered. Peduncle to 2.1 cm long and pedicel to 2.3 cm long; both green, glabrous, and with raised longitudinal ridges. Calyx during anthesis: green, 5.2–7.4 mm from pedicel to tip of lobe, 12–14 mm diam., the midrib raised, ciliolate near apex with 1- to 3-celled finger hairs 38–138 μm long, the hairs usually simple but occasionally with more than one terminus, abaxially with abundant stalked glands 60–75 μm long. Calyx at fruit maturity: to 26 mm diam., stellate, green, rotate to slightly reflexed, not hiding fruit in side view. Corolla (Fig. 2B) rotate, light green with dark-green maculae collectively stellate in outline, 5-lobed, 17–20 mm (–25 mm, cultivated) diam., the margin ciliolate with branchlet hairs to 190 μm long, adaxially densely pilosulose with erect, gland-tipped (droplet-tipped on fresh flowers) finger hairs, (4)5- to 6-celled and 210–290 μm long, abaxially with abundant stalked glands 70–80 μm long. Stamens (Fig. 3C) 4.5–5 mm long; filaments straight or nearly so, nearly glabrous with unpigmented finger hairs to 0.3 mm long only on expanded base; anthers (Fig. 3D) 1.4–1.9 × 1.0–1.8 mm, yellow. Pollen 25–27.5 μm diam. (n = 59 grains); 74,000–149,000 grains per androecium (n = 2 androecia). Stigma green, capitate, with a shallow medial groove (when living), 0.33–0.51 mm wide (when pressed), the papillae to 28 μm long (living); style 4.2–5.1 mm long, curving and so orienting the stigma to the side (Fig. 2B); ovary dark green with an off-white to light orange disk girdling the base, glabrous; 158–168 ovules per ovary (n = 2 ovaries). Mature berries dark black-blue, subspherical, to 14 mm diam. (similar to Fig. 2F). Seeds subovate, alveolate, 1.8–1.98 × 1.41–1.62 × 0.45–0.54 mm thick, to 146 per fruit. Chromosome number 2*n* = 24.

Paratypes. COSTA RICA. **Guanacaste:** Santa Rosa National Park, ca. 10°50′N, 85°37′W, 0–320 m, 16 July 1981, *Janzen 12113* (MO); 10°50′N, 85°35′W, 8 Nov. 1981, *Janzen 12125* (F); Nicoya Peninsula, Cantón Nandayure, Pilas de Bejuco, Quebrada Seca, 9°52′01″N, 85°20′45″W, 40 m, 15 Oct. 1994,

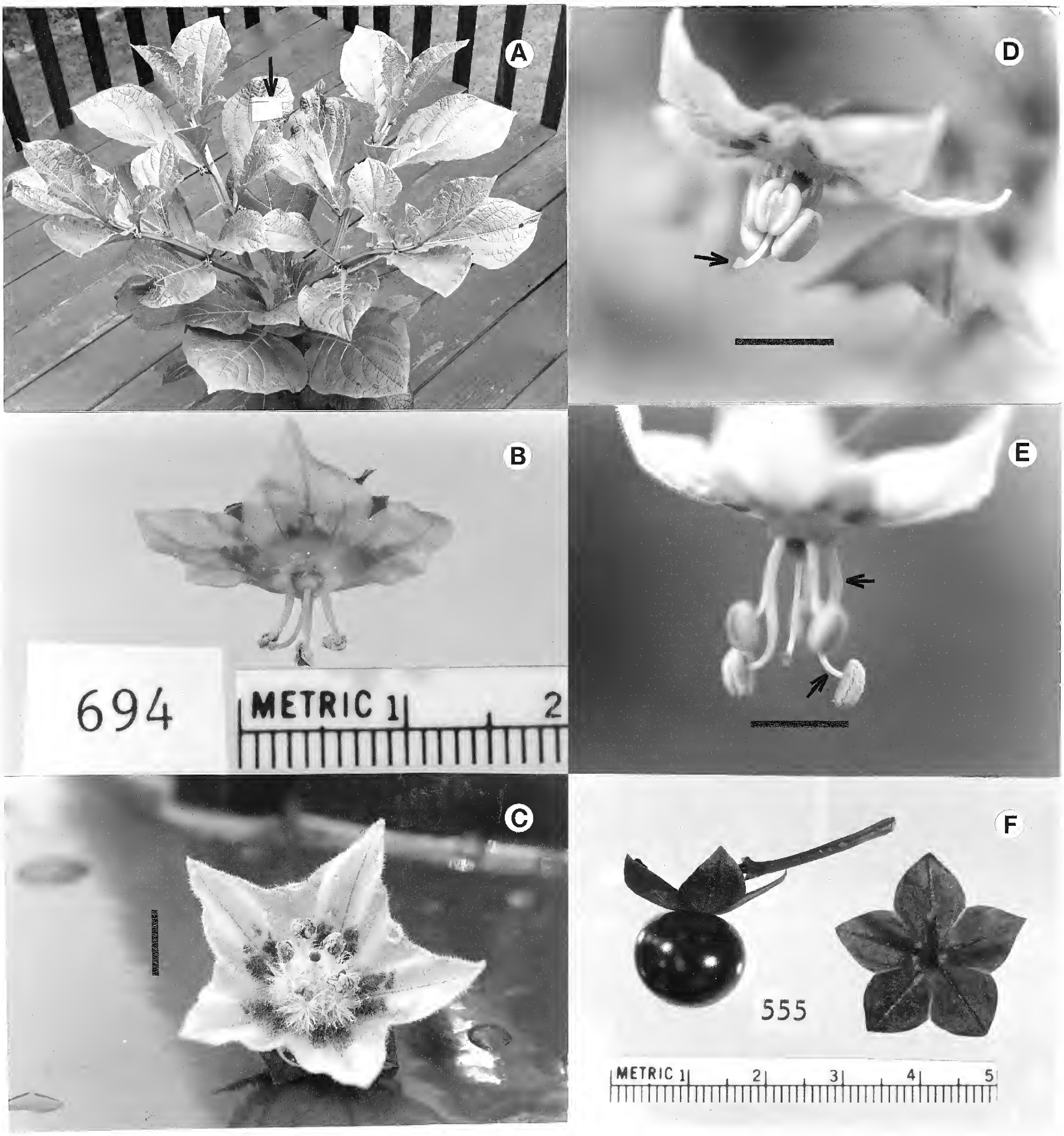

Figure 2. ***Jaltomata*** of Costa Rica. A, B. ***J. darcyana, Mione & Yacher 694.*** —A. Note erect habit, nearly entire leaves, and strongly angled stems. White scale bar (at arrow) = 6 cm. —B. Flower with two stamens removed to show curved style; note nectar where androecium meets corolla. —C. Flower of ***J. procumbens***, ***Bohs' seed 96-49***. Note the straight style and straight filaments; anthers have dehisced; stigma at center; bar = 5 mm. D, E, F. ***J. repandidentata.*** —D. ***Mione & Yacher 605***. Flower in pistillate phase: the first day the flower is open filaments remain short and anthers undehisced; note anther size variation, variation in length of stamens, curved style orienting bilobed stigma (at arrow) to side; bar = 5 mm. —E. ***Mione & Yacher 605***. Hermaphroditic phase, filaments have elongated and those of the longer stamens are sigmoid; two arrows point to one filament; the anthers of the longest stamens have dehisced; style curving stigma toward viewer; bar = 5 mm. —F. ***Mione & Coe 555.*** Black-purple berry with calyx (left), and calyx with abaxial face and pedicel showing (right).

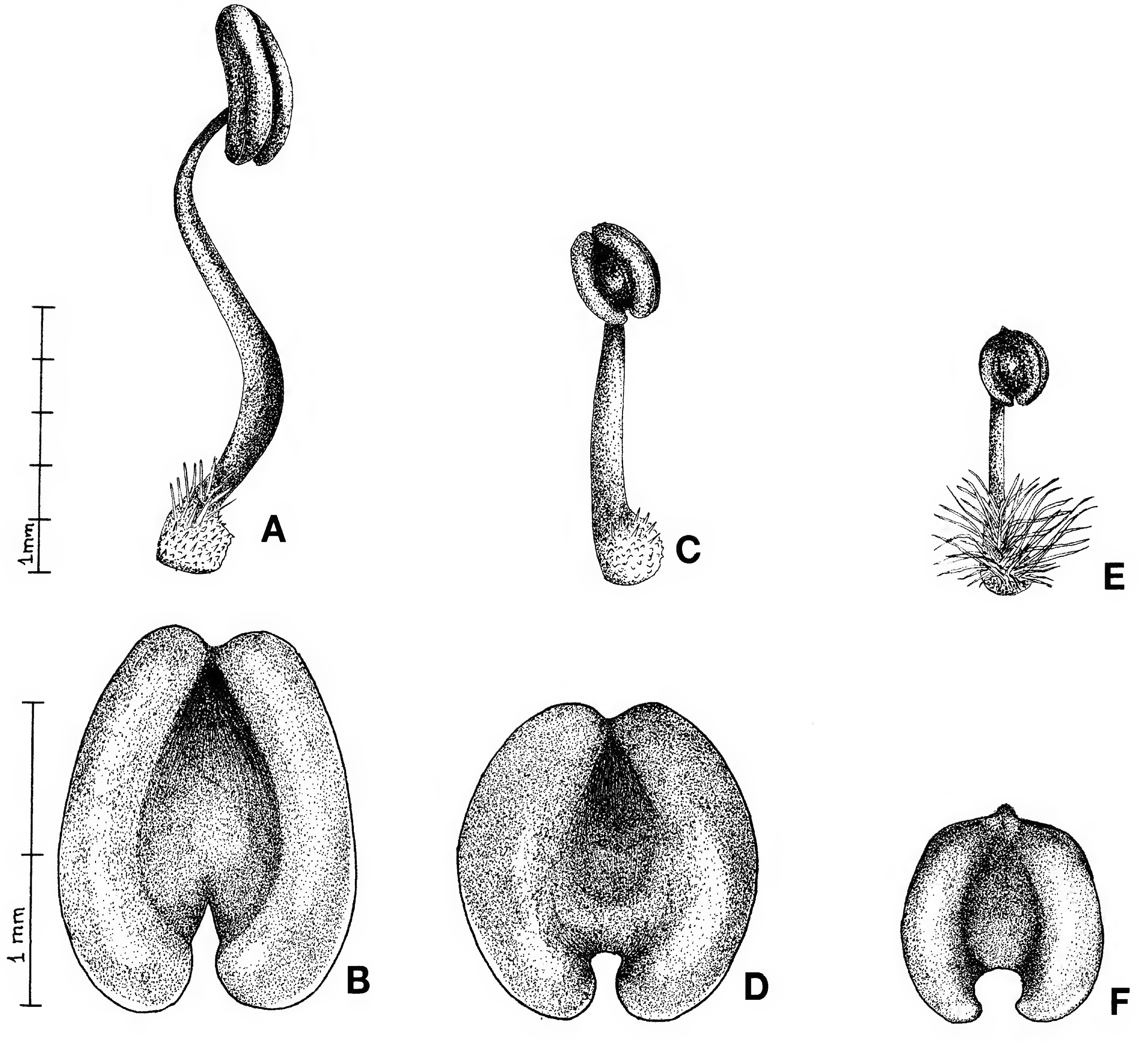

Figure 3. Stamens (tangential view) and anthers (dorsal face). A, B. ***Jaltomata repandidentata*, *Mione & Yacher 605***. —A. Sigmoid filament with anther. —B. Anther. C, D. ***J. darcyana, Mione & Yacher 694***. —C. Nearly straight filament with anther. —D. Anther. E, F. ***J. procumbens, Mione et al. 699***. —E. Straight filament with mucronate anther. —F. Mucronate anther. Illustration by Luis Serazo.

Estrada & Rodríguez 242 (CR, INB). **Puntarenas:** Reserva Biológica Carara Estación Quebrada Bonita, 9°46′N, 84°36′W, 30 m, 26 June 1990, ***Bello & Rojas 2295*** (CR, F, INB); Nicoya Peninsula, Curú, pastures S of entrance road, mouth of Marianas Canyon, 50 m, 13 Sep. 1995, ***Sanders & Baker 17892*** (F, NY).

REPRODUCTIVE BIOLOGY OF *JALTOMATA DARCYANA*

This species is self-compatible and autogamous, based on abundant fruit production by spatially isolated plants grown for study in 2000, 2001, and 2002. Translucent nectar droplets were observed where the corolla and androecium meet (Fig. 2B). This nectar is very likely produced by the ovarian disk and then, taking the path of least resistance, seeps through the bases of the stamens on to the corolla. Flowers of this species last only a single day during which they are functionally perfect.

Jaltomata procumbens (Cav.) J. L. Gentry, Phytologia 27: 287. 1973. *Atropa procumbens* Cav., Icon. Pl. 1: 53, t. 72. 1791. *Saracha procumbens* (Cav.) Ruiz & Pav., Fl. Peruv. Prodr. 2: 43. 1794. TYPE: Cavanilles, Icon. Pl. 1: 53, t. 72. 1791 (lectotype, designated here).

Jaltomata edulis Schltdl., Hortus Halensis 8. 1838. TYPE: "Prope los baños del grande indefessus C. Ehrenberguis fructiferam Octoberi mense carpsit," ***Ehrenberg s.n.*** (not seen).

In Costa Rica *Jaltomata procumbens* (Figs. 2C, 3E, F) is common at higher elevations along the edges of trails and roads. This species is somewhat scattered in Figure 1 because of the morphological variation present among the collections utilized from a large geographic area (Mexico, Guatemala, and Costa Rica). In Mexico it is a common weed in agricultural fields where it is deliberately not weeded out so that fruits can be gathered for consumption (Davis & Bye, 1982) and sometimes sold in markets (R. Bye, pers. comm.).

Two races of *Jaltomata procumbens* grow sympatrically, and were found only 4 m apart in Parque Nacional Tapantí (hereafter, Tapantí). One race is glabrous and has longer peduncles (to 6 cm) and nearly entire leaves. This race is common along the edge of the gravel road in Tapantí (*Mione & Yacher 687*) and was found on the Continental Divide at Monteverde (*Mione 583, 606*), observed along trails in the Santa Elena reserve (not collected), and was collected at Río La Paz Pequeña (*Bohs 95-4*). The other race, in contrast, is pubescent and has shorter peduncles and toothed leaves. This race was collected at Tapantí (*Mione & Yacher 686, 688*), and in the Monteverde area: (1) at Catarata San Luis (*Bohs 96-49*), (2) as an epiphyte in the primary forest (*Mione & Haber 697*), and (3) outside the main reserve on a road bank (*Mione & Haber 698*). The two collections of the glabrous race used in the PCA group together (Fig. 1). The epiphytic *J. procumbens* collected (pubescent race) was a light gap colonist in a primary Tropical Lower Montane Wet Forest at Monteverde (W. Haber, pers. comm.; see Holdridge et al., 1971). It is clear that the races have overlapping niches, and further study will be necessary to determine the taxonomic level, if any, at which these races should be recognized.

Uses. During fieldwork for this study, only at a population near the summit of Volcán Turrialba were we informed by a resident that fruits are eaten. The label of one other specimen (*Holway 283*) of this species indicates that the fruits are used in Costa Rica, and gives the local name "yerba mora."

Selected specimens examined. COSTA RICA. **Puntarenas:** Monteverde, upper community, lower montane wet forest, epiphyte herb on tree trunk, 27 Sep. 1985, ***Haber 2804*** (MO). **Border of Puntarenas and Alajuela:** Cordillera de Tilarán, on & near Continental Divide, ca. 2–5 km E & SE of Monteverde, along trail below windswept elfin forest, 17 Mar. 1973, ***Gentry & Burger 2737*** (MO). **Alajuela:** Monteverde Reserve, Atlantic Slope, Río Peñas Blancas valley, ridge trail above Quebrada Leona, forest edge, 17 Jan. 1985, ***Haber 1317*** (MO); Alajuela, region of Zarcero, 29 Sep. 1937, ***Smith A457*** (F). **Heredia:** Vara Blanca de Sarapiqui, N slope of Central Cordillera, July–Sep. 1937, ***Skutch 3188*** (GH, NY, US). **San José:** along Interamerican hwy. betw. Villa Mills and San Isidro de El General, km 111, ***Grayum et al. 3428*** (MO); Las Nubes, 20–22 Mar. 1924, ***Standley 38651*** (US); Cordillera de Talamanca, reserva Privada Cerros de Escazú, Finca El Cedral, 8 Aug. 1996, ***Cascante 1107*** (CR, F). **Cartago:** El Muñeco, Río Navarro, 6–7 Mar. 1926, ***Standley & Torres R. 1158*** (US); Parque Nacional

Tapantí, along road 1.2 km after entrance, 11 Dec. 1996, ***Spooner et al. 7126*** (INB not seen, WIS not seen, herbarium of T.M.); ca. 10 km S of Tapantí above Río Grande de Orosi, 10–24 June 1968, ***Burger & Stolze 5725*** (F, NY); Cordillera de Talamanca, along road from bridge over Río Grande de Orosi (near jct. with Río Villegas) to Río Humo, 11 Aug. 1984, ***Grayum et al. 3743*** (MO); SW slope of Volcán Irazu, W of Sabanilla, 7 Mar. 1987, ***Burger et al. 12079*** (F, MO, NY); Volcán Irazu, 23 Dec. 1915, ***Holway 283*** (US); Volcán Turrialba, 13 Dec. 1996, ***Spooner et al. 7132*** (INB not seen, herbarium of T.M.).

Jaltomata repandidentata (Dunal) Hunz., Kurtziana 10: 8. 1977. *Saracha procumbens* var. *repando-dentata* Dunal, Prodr. 13(1): 431. 1852. *Saracha repandidentata* (Dunal) Bitter, Repert. Spec. Nov. Regni Veg. 19: 269. 1924. TYPE: Peru. *Poeppig 1419* (holotype, F!; isotypes, G!, photo of destroyed B specimen, F neg. 2555, GH!, WIS!; W, photo of W specimen, F neg. 33015, GH!, WIS!).

This species has not been previously reported from Central America, yet it is clearly morphologically distinct (Figs. 1, 2D–F, 3A, B). Growing from Mexico to Bolivia, it is a common weed in coffee plantations, based on: (1) fieldwork by T.M. with associates in Nicaragua and Bolivia, (2) plants grown from seeds collected in the shade of coffee in Mexico (Table 1), and (3) study of herbarium specimens. In Costa Rica we collected this species in coffee plantations, and along the roadside on the Pacific slope on the way up to Monteverde.

With living material or flowers preserved in alcohol *Jaltomata repandidentata* is easily distinguished from other species of the genus. Throughout its range *J. repandidentata* is characterized by: (1) size variation among anthers of a flower, most evident during the first day the flower is open when anthers remain undehisced (Fig. 2D), (2) stamen length variation within each flower during both the initial pistillate phase when filaments are short (Fig. 2D) and the perfect phase after filaments fully elongate (Fig. 2E), (3) longer stamens finally sigmoid (Fig. 2E, 3A), (4) curved style orienting the stigma to the side (Fig. 2D, E), (5) stigma shallowly grooved to bilobed (Fig. 2D), (6) larger anthers dehisce earlier than smaller anthers of the same flower (Fig. 2E), and (7) fruit fully exposed (the calyx does not hide it) in a view perpendicular to the pedicel at the height of the fruit (Fig. 2F). All of these features were seen on the collections of *J. repandidentata* listed in Table 1, all studied in the living condition. Unfortunately, these characters are often obscured on pressed specimens. For example, anther size variation is much less evident after anthers dehisce. Filaments usually appear curved on pressed specimens, but the straight filaments of other species may become curved during pressing. Similarly, the straight style of *J. procumbens* may become curved during pressing. Unfortunately, if a stigma is flattened during pressing it will not appear bilobed, even though grooved to bilobed stigmas are characteristic of *J. repandidentata*.

Uses. In Costa Rica the label of one specimen reads "Fruto comestible" and gives the local name "yerba de mora" (*Brenes 12*). In Guatemala plants of this species were "used as a pot herb by Indians" (*Muenscher 12458*, BH, and *12479,* BH F). In Peru the fruits were described as edible (*Cowgill 1079,* BH GH).

Selected specimens examined. COSTA RICA. **Alajuela:** N of San Ramon on NE slopes at bridge over Río Barranca, in coffee plantation, 17 June 1976, ***Davis 616*** (MO); Tacares, Río Prendas bridge on rt. 1 to Alajuela under coffee just before river, 18 June 1976, ***Davis 623*** (MO). **Heredia:** betw. Santo Domingo and Río Virilla, 6 Jan. 1974, ***Lent 3756*** (F). **San José:** Jardinería en San José, ***Brenes 12*** (F); vicinity of El General, June 1936, ***Skutch 2649*** (GH, K, NY, US); vicinity of El General, June 1939, ***Skutch 4373*** (F, GH, K, NY, US). **Cartago:** S of San Isidro de General on Rt. 2 at Río Jilguero in coffee and banana plantations, 14 June 1976, ***Davis 613*** (MO); San Isidro de General, 24 July 1940, ***Chrysler 5293*** (F).

DISCUSSION

The *Flora of Costa Rica* (Standley, 1937) lists a single species of the genus *Jaltomata*, *J. procumbens*, as did Janzen and Liesner (1980) and Pittier (1908). In contrast, the results of this study support the recognition of three species of this genus in Costa Rica.

This study brings the number of recognized *Jaltomata* species of the United States (Arizona), Mexico, and Central America to six: *J.*

chihuahuensis (Bitter) Mione & Bye (northern Mexico); *J. confinis* (Morton) J. L. Gentry (Guatemala); *J. grandiflora* (Michoacán, Mexico); and the species discussed here.

Based on the results of this study a new species of the seasonally dry Pacific Coast, *Jaltomata darcyana*, is described. This species is morphologically distinct (Fig. 1), grows at lower elevations than the other species, and its DNA places it outside the clades that include *J. procumbens* and *J. repandidentata.* The flowers of all other *Jaltomata* of Mexico and Mesoamerica studied to date, some 50 collections, last at least two days and are always pistillate for a day prior to filament elongation and anther dehiscence. In contrast, *J. darcyana* has lost this initial period during which the flower cannot self-pollinate.

KEY TO THE *JALTOMATA* OF COSTA RICA

1a. Style straight; in Costa Rica calyx at flowering green with purple lobe tips and/or purple main veins; anthers of uniform size, mucronate in Costa Rica (Fig. 3E, F); mature fruit partially hidden by calyx on some collections; 1000–2900 m...*J. procumbens* (Cav.) J. L. Gentry

1b. Style curved (Fig. 2B, D); calyx at flowering uniformly green; anthers neither mucronate nor mucronulate, those of a flower vary in size (most evident during the first day the flower is open when anthers remain undehisced); fruit fully exposed (the calyx does not hide it) in a view perpendicular to the pedicel at the height of the fruit, as shown for *J. repandidentata* in Figure 2F.

2a. Leaves membranous, to 20 cm long; filaments curved to sigmoid (Fig. 2E); stigma shallowly grooved to bilobed (Fig. 2D); flowers pistillate for a day and then functionally perfect; 400–1200 m...*J. repandidentata* (Dunal) Hunz.

2b. Leaves somewhat coriaceous, to 30 cm long; filaments straight or nearly so (Fig. 2B); stigma with a very shallow medial groove; flowers functionally perfect when they open; 0–320 m...*J. darcyana* Mione

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The specific epithet "*darcyana*" was chosen to honor William D'Arcy. Bill generously and patiently shared his expertise and treated me like a valued colleague even when I was a novice researcher. Bill will always be remembered and always be missed. T.M.

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7

THE SOLANACEAE OF THE *LOMAS* FORMATIONS OF COASTAL PERU AND CHILE

Michael O. Dillon

ABSTRACT. The western coast of South America [5–30°S lat] is dominated by desert conditions that form a continuous, hyper-arid belt, broken only by occasional river valleys. The native, non-riparian vegetation of these deserts is largely confined to localities where recurring fogs meet the near-shore terrain. The fogs supply moisture for the development of plant communities here termed *lomas* formations. The *lomas* formations range over 3500 km and contain a combined vascular flora of over 1400 species. Individual *lomas* formations are isolated and endemism is high, reaching over 40% in some localities. This paper summarizes the current state of knowledge on the distribution and origin of the family Solanaceae within the *lomas* formations. The family is represented by 18 genera and 128 species arrayed in five subfamilies: Cestroideae, Nicotianoideae, Petunioideae, Schizanthoideae, and Solanoideae. Among the genera with endemic species are *Exodeconus*, *Grabowskia*, *Jaltomata*, *Leptoglossis*, *Lycium*, *Nicotiana*, *Nolana*, *Reyesia*, *Schizanthus*, *Salpiglossis*, and *Solanum* (including *Lycopersicon*). No fewer than 90 endemic species are recorded from the *lomas* formations, and *Nolana*, with 70 endemic *lomas* species, stands out as the largest and most wide-ranging genus of the *lomas* flora and the only genus to be encountered in all *lomas* formations. Different biogeographic patterns, i.e., autodisjunctions and allodisjunctions, are displayed and these reflect different arrival times and origins for the members of this specialized floristic community. Short-term climatic fluctuations, such as El Niño events, and long-term climatic change associated with glacial cycles have been influential in expansions and contractions in the floras of the Andean Cordillera.

Key words: Atacama Desert, biogeography, Chile, El Niño, *lomas* formations, Peru, Peruvian Desert, Solanaceae.

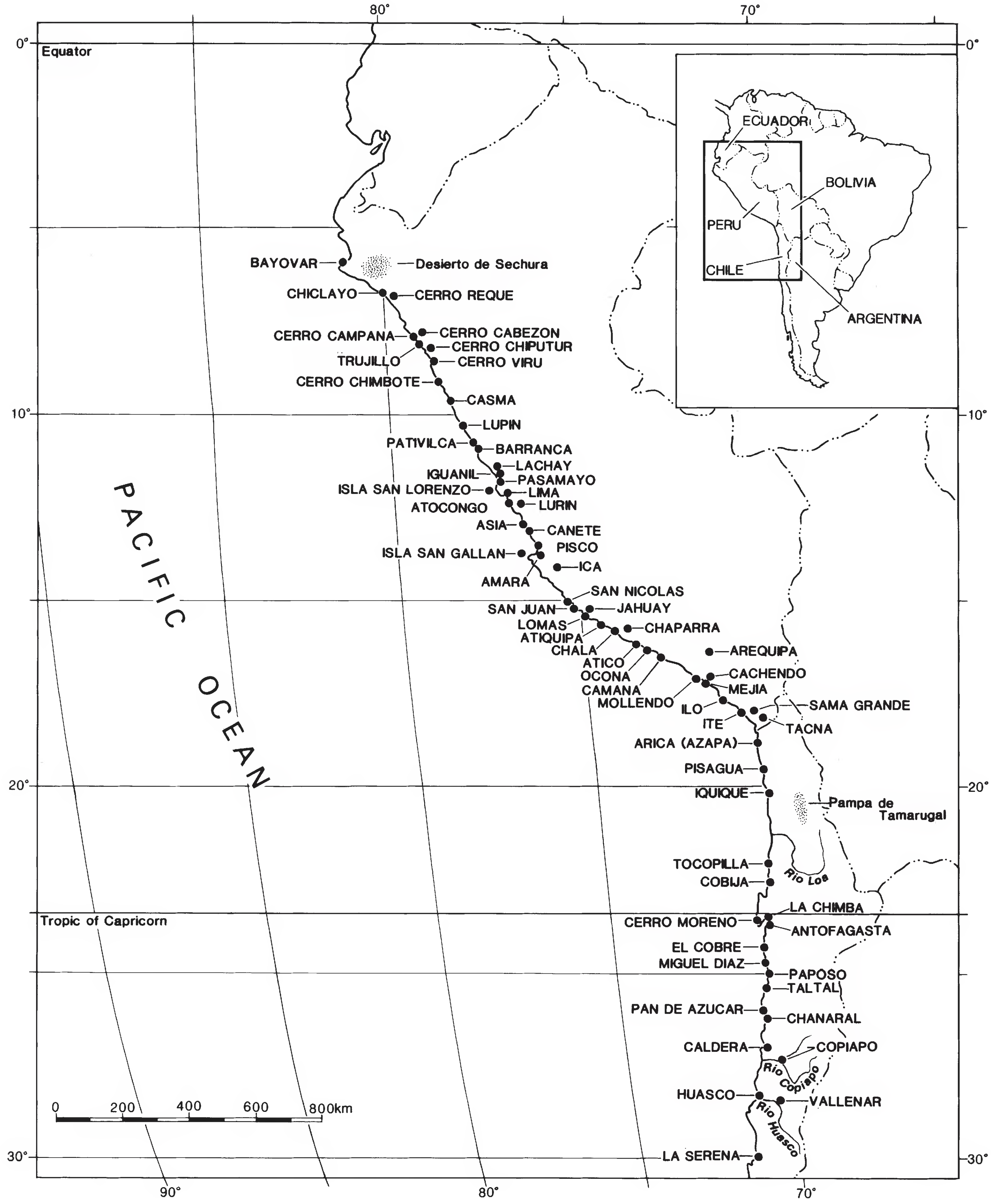
For nearly 3500 km along the western coast of South America [5°–30°S latitude], the Atacama and Peruvian Deserts form a continuous, hyper-arid belt, broken only by occasional river valleys from the Andean Cordillera. Though this is one of the driest places on Earth, it is home to an extraordinary type of vegetation termed *lomas* formations (Dillon, 1997; Dillon & Hoffmann, 1997; Rundel et al., 1991). These highly endemic plant communities occur in near-shore locations where ocean fog provides sufficient moisture for the development of vegetation. Each locality is an island of vegetation among a virtual ocean of arid desert, and over 100 such localities have been identified from northern Peru to central Chile (Fig. 1). The size and topography of individual formations vary greatly, as does the distance between formations. Rundel et al. (1991) provided a detailed discussion of the climate, geomorphology, and vegetation of this region, but a brief review of the major points is warranted for the current discussion.

COASTAL CLIMATE AND EL NIÑO EVENTS

Various factors are responsible for the development of the hyper-arid conditions along the coasts of Chile and Peru. All of western South America is isolated from weather patterns to the east by the Andean Cordillera, which reaches an average height of over 3500 m. Temperatures are homogeneous along the entire latitudinal extent of the deserts, which results from the influence of cool, sea surface temperatures associated with the south to north flow of the Humboldt (Peruvian) Current. This, combined with the positionally stable, subtropical anticyclone, results in a mild, uniform coastal climate where it nearly never rains, but there is the regular formation of thick stratus clouds below 1000 m usually during the months of September to December.

In addition to these seasonal fogs, the coastal region is also influenced by periodic and recurrent El Niño Southern Oscillation (ENSO) events. The frequency of El Niño events is roughly every 30 to 50 years for major events and every 3.5 to 7 years for minor events; however, two of the strongest El Niño events were recorded in 1982/1983 and 1997/1998. The El Niño phenomenon is complex and a complete explanation is beyond the scope of this paper (Allan et al., 1996). But simply put, El Niño conditions prevail when the normally cold waters off the coast of western South America are displaced by warmer water originating in the western Pacific. These conditions stimulate brief periods of heavy rainfall and relatively high temperatures. The increase in available moisture has profound effects upon the *lomas* formations and undoubtedly shapes their composition and structure. This is manifested by the stimulation of massive blooming events that replenish seed banks for annual and perennial plants. This phenomenon is illustrated with two photographs taken from approximately the same spot at the base of Cerro Cabezón in northern Peru. During a non-El Niño year (Fig. 2A), terrestrial *Tillandsia* (Bromeliaceae) dominates. But, during the 1997/1998 El Niño events, the foreground contains a dense population of *Exodeconus maritimus* (Solanaceae) (Fig. 2B). This white-flowered, prostrate annual can have branches reaching nearly three meters in length when sufficient moisture is available.

It is difficult to imagine what the coastal vegetation would resemble in the prolonged absence of El Niño events. One effect might be the reduction in levels of floristic diversity and elimination of migration and establishment within and between formations. Data relating to the historical onset of El Niño conditions suggest that the phenomenon can be accurately dated to between 5000 and 15,000 years ago (Fontugne et al., 1999; Rodbell et al., 1999). Longer-term records of El Niño events are more difficult to establish, but results from fossil coral suggest that El Niño-like conditions may have existed for over 100,000 years (Hughen et al., 1999). Authors have argued that the present extent of coastal aridity of the Atacama and Peruvian deserts is quite young (Arroyo et al., 1990), perhaps Holocene age (10,000 bp), while others suggest much greater antiquity but influenced by pluvial cycles (Alpers & Brimhall, 1988; Betancourt et al., 2000; Rundel


80°
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0°
Equator
ECUADOR
BOLIVIA
PERU
CHILE
ARGENTINA
BAYOVAR
Desierto de Sechura
CHICLAYO
CERRO REQUE
CERRO CAMPANA
CERRO CABEZON
CERRO CHIPUTUR
TRUJILLO
CERRO VIRU
CERRO CHIMBOTE
CASMA
10°
LUPIN
PATIVILCA
BARRANCA
LACHAY
IGUANIL
PASAMAYO
ISLA SAN LORENZO
LIMA
ATOCONGO
LURIN
ASIA
CANETE
PISCO
ISLA SAN GALLAN
ICA
AMARA
PACIFIC OCEAN
SAN NICOLAS
SAN JUAN
JAHUAY
LOMAS
ATIQUIPA
CHAPARRA
CHALA
ATICO
AREQUIPA
OCONA
CACHENDO
CAMANA
MEJIA
MOLLENDO
ILO
SAMA GRANDE
ITE
TACNA
ARICA (AZAPA)
PISAGUA
20°
IQUIQUE
Pampa de Tamarugal
TOCOPILLA
COBIJA
Rio Loa
LA CHIMBA
Tropic of Capricorn
CERRO MORENO
ANTOFAGASTA
EL COBRE
MIGUEL DIAZ
PAPOSO
TALTAL
PAN DE AZUCAR
CHANARAL
CALDERA
COPIAPO
Rio Copiapo
HUASCO
VALLENAR
Rio Huasco
0 200 400 600 800km
30°
LA SERENA
90°
80°
70°

Figure 1. Geographic features, including *lomas* localities referred to within the Atacama and Peruvian Deserts.

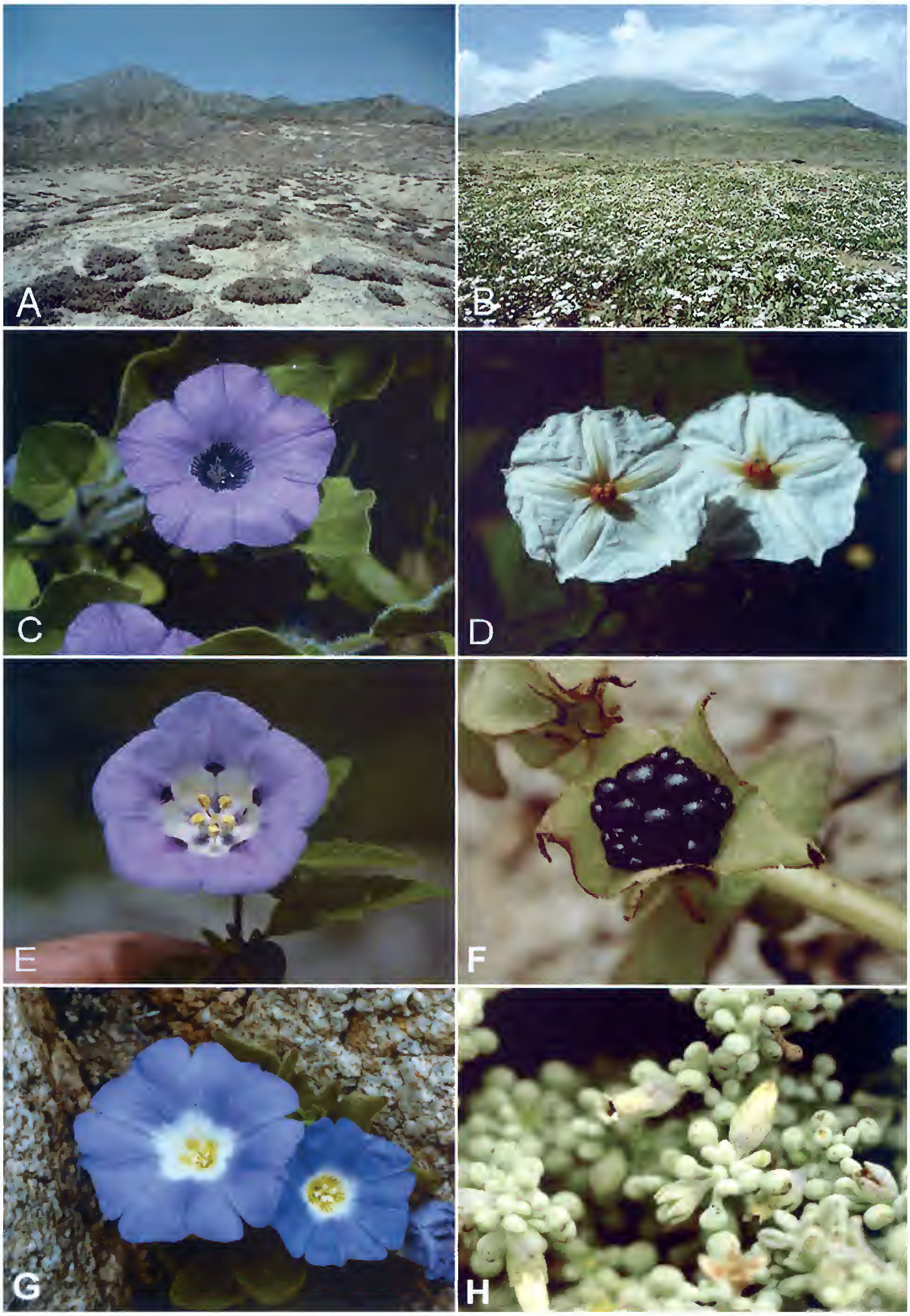

Figure 2. Solanaceae of the *lomas* formations. —A. Photograph of Cerro Cabezón (Dept. La Libertad, Peru) during a dry, "non-El Niño" period (June 1998). Only colonies of perennial, terrestrial *Tillandsia latifolia* are evident in the foreground. —B. Photograph of Cerro Cabezón during a wet, El Niño phase (February 1998) with annual, white-flowered *Exodeconus maritimus* in foreground. —C. *Exodeconus prostratus* flower (*Lomas* of Lupín, Peru). —D. *Lycianthes lycioides* flower from Cerro Campana. —E. *Nicandra physalodes* (Virú, Dept. La Libertad, Peru). —F. Mericarps in *Nolana rupicola* (Parque Nacional Pan de Azúcar, Antofagasta, Chile). —G. *Nolana rupicola* flowers (Parque Nacional Pan de Azúcar). —H. *Nolana peruviana* illustrating succulent, reduced leaves and reduced flowers (Caleta Buena, Antofagasta, Chile).

et al., 1991). Regardless of their age, recurrent El Niño events have surely helped shape the coastal communities present today (Dillon et al., 2003; Dillon & Rundel, 1990; Holmgren et al., 2001).

FLORISTIC STUDY

The study area, as defined here, is the *lomas* formations, which refers to fog-dependent, near-shore vegetational communities from northern Peru (ca. 7°S) to north-central Chile (ca. 28°S) (Dillon, 1997; Dillon & Hoffmann, 1997; Rundel et al., 1991). The plant communities are distributed between sea level and 1000 m, and usually within 1–30 km of the coast. Though the term *lomas* formations was originally proposed for southern Peruvian plant communities (Weberbauer, 1945), it is here used for all the communities along the coast that correspond to this definition. Other terms applied to these formations include "fertile belt" (Johnston, 1929), "meadows on the desert" (Goodspeed, 1961; Goodspeed & Stork, 1955), "oasis de niebla" (Ellenberg, 1959; Muñoz-Schick et al., 2001), and "desierto costero" (Gajardo, 1987).

The author's study of the flora of the *lomas* formations has been under way since 1983, with the desert-blooming display during the 1982/1983 El Niño event. Over the last 20 years, fieldwork and collecting have been conducted throughout the extent of the *lomas* formations, including a series of collecting trips during and after El Niño events in Chile and Peru. Nearly 2100 collections have been made and all major herbaria with holdings from the region have been consulted. From these efforts, a database, called LOMAFLOR, was established and currently contains nearly 9000 specimen records representing ferns, gymnosperms, monocotyledons, and dicotyledons recorded from the *lomas* formations. LOMAFLOR is available via the internet <http://www.sacha.org/search_frame.htm>.

The native, non-riparian, vascular flora confined to these localities consists of 108 families, 520 genera, and ca. 1400 species. For this treatment, nearly 1600 herbarium sheets of Solanaceae have been consulted, and virtually all the species treated here have been observed, collected, and photographed in their respective environments. The Solanaceae of the coastal deserts of Chile and Peru comprise 18 genera and 128 species and rank as the second most species-rich family in the flora of the *lomas* formations. Only the Asteraceae, with 57 genera and nearly 150 species, contain more diversity within the *lomas* communities. The *lomas* formations contain pantropical species, a few Northern Hemisphere desert disjunctions, Andean Cordillera disjunctions, and a complement of genera and species endemic to the *lomas* formations. Endemic taxa can be widespread in several *lomas* formations or restricted to a single locality. Endemism in the overall flora often exceeds 40% in individual localities (Duncan & Dillon, 1991) and in the Solanaceae of the *lomas* formations, ca. 70% (90 of 128 species) are considered endemic (cf. Appendix 1).

Vegetation in the coastal deserts of western South America is not uniformly distributed (Rundel et al., 1991). It appears that there are at least three primary floristic segments within the coastal deserts that reflect independent histories: a northern Peruvian unit from ca. 7°S to 13°S latitude, a southern Peruvian unit from 13°S to 18°S latitude, and a northern Chilean unit from 20°S to 28°S latitude. The segment of coastal desert in extreme northern Chile, between 18° and 20°S latitude, is a hiatus, nearly devoid of vegetation, that lacks the proper, near-shore topography to develop *lomas* communities (cf. Rundel & Dillon, 1998; Rundel et al., 1991). In the overall *lomas* flora there are two centers of species endemism, one in southern Peru (13°–18°S) and the other in northern Chile (20°–28°S). There is a distributional hiatus between the modern desert floras of northern Chile and southern Peru. An analysis of the entire vascular plant flora from the coastal desert shows that only 112 species, from a total of ca. 1400, have distributions in both Peru and Chile. If widespread or weedy species are eliminated from the analysis, only 93 non-introduced species cross the 18°–20° latitude boundary, suggesting little active exchange over the hyper-arid barrier or hiatus. (An illustration representing the sectoring of the coastal flora in Peru and Chile is available via the internet, <http://www.sacha.org/famil/nolana/Nolana_sectoring.htm>.)

BIOGEOGRAPHIC PATTERNS

The biogeography of the Solanaceae was analyzed and discussed by D'Arcy (1991). South America is a center of generic and species diversity (Hunziker, 1979, 2000), and the family is considered to be of Gondwanan origin (Symon, 1991). Studying the potential biogeographic relationships among *lomas* representatives allows the development and testing of hypotheses concerning the origins of these species. Our ability to reconstruct these events in an area the size of the Atacama and Peruvian Deserts requires information from many sources, including distributional patterns, information on past climates, and reconstructed phylogenies of member organisms.

There are few phylogenetic studies for genera represented within the Solanaceae of the *lomas* formations. At the family level, molecular studies (Olmstead & Palmer, 1992; Olmstead et al., 1999) have included 16 genera with *lomas* representatives. Species-level studies have been completed or are under way in several genera with *lomas* representatives (see below). The subfamilial and tribal circumscriptions are still being formulated (D'Arcy, 1991; Hunziker, 1979a, 2000a) and differences of opinion are evident (Olmstead et al., 1999; Hunziker, 2001). The categories presented here are intended for discussion of distributional patterns and potential biogeographic origins. Terminology for the description of disjunctions follows Turner (1972: 153). Autodisjunctions (autojuncts) are defined as "two or more morphologically similar populations that are widely separated spatially, the more remote elements having become isolated through the dissemination of appropriate colonizers from some *extant* population or gene pool." This type of disjunction is typically the result of a long-distance dispersal event, but vicariant events can accomplish the same distributional pattern (Wen et al., 2002). Continuing, allodisjunctions (allojuncts) are "two or more closely related populations (i.e., more closely related to each other than either is to yet some other taxon) that are widely separated spatially, the various elements of which have been derived through phyletic divergence from populations now *extinct*."

The genera distributed in the *lomas* formations are arrayed in five subfamilies in the Solanaceae: Cestroideae, Petunioideae, Nicotianoideae, Schizanthoideae, and Solanoideae. Figure 3 provides a simplified tree, adapted from a strict consensus cladogram in the analysis conducted by Olmstead et al. (1999: 125). What follows here is a brief discussion of the Solanaceae of the *lomas* formations in relation to their classification in subfamilies, tribes, subtribes, and sections, and the current state of knowledge concerning their phylogenetic positions.

SCHIZANTHOIDEAE

The Schizanthoideae are monotypic with *Schizanthus* containing 12 species and distributed from northern to southern Chile and one species reaching Argentina (Coccuci, 1989). Four species range into northern Chile, where two species are endemic to the *lomas* formations and another two species are found immediately to the south, where they only just reach the edge of the Atacama Desert (Grau & Gronbach, 1984). Olmstead et al. (1999) concluded that *Schizanthus* is an early-diverging lineage within the Solanaceae and basal to the remainder of the family. Peña and Muñoz (2002) provided a species-level phylogeny for *Schizanthus* based upon morphological and alkaloid chemical characters. Their results suggested two species groups: one with white flowers without nectar guides, explosive pollen release, and pollination by nocturnal moths, and another with lavender flowers, nectar guides, passive pollen release, and pollination by bees. In the *lomas* formations, *S. integrifolius*, *S. lacteus*, and *S. candidus* are found in the white-flowered group, and *S. laetus* is found in the lavender-flowered group. Peña and Muñoz (2002) stated that the white-flowered species are the more primitive and likely ancestral to the lavender-flowered group. Further, they

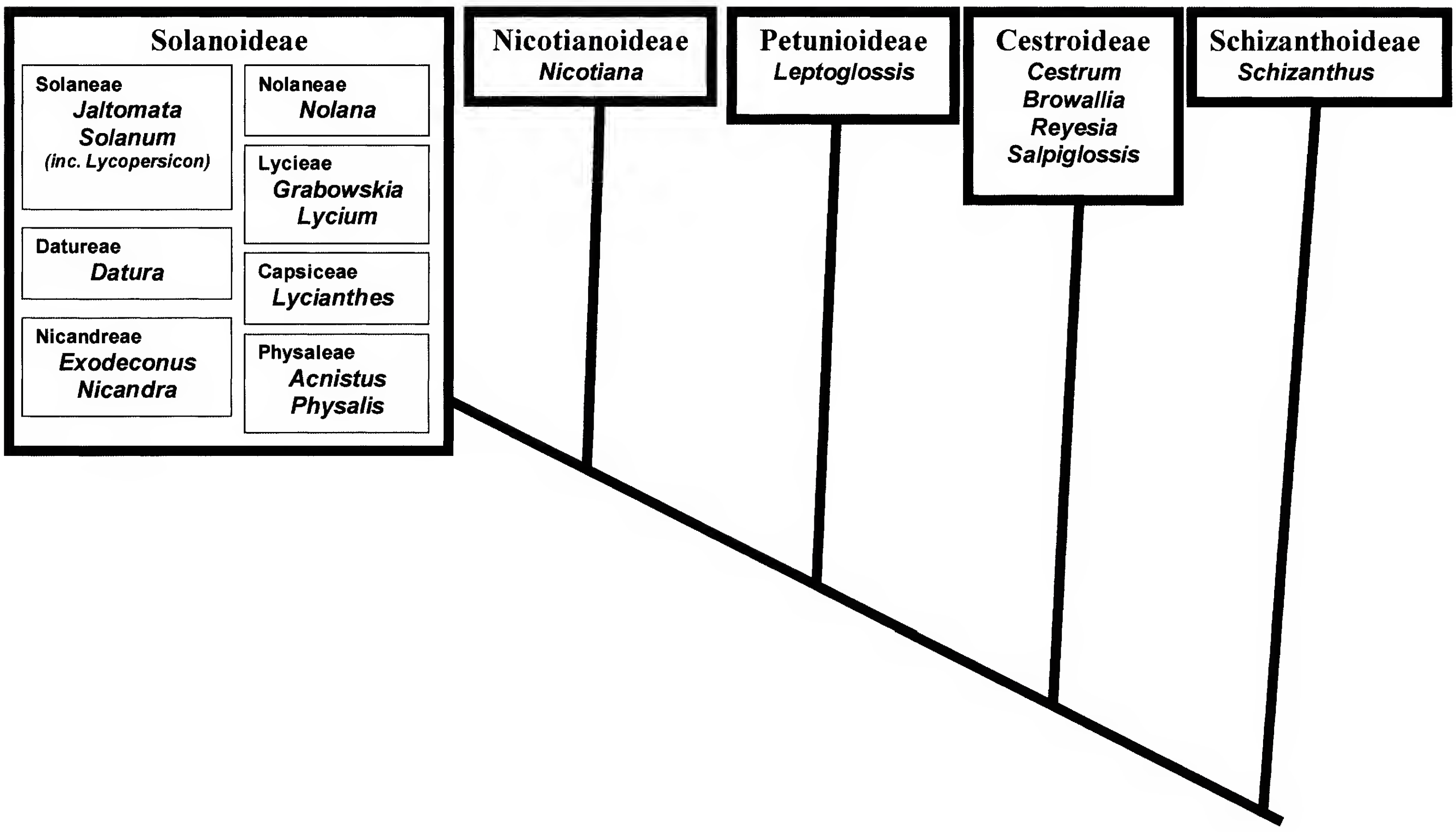
Solanoideae
Solaneae
Jaltomata
Solanum
(inc. Lycopersicon)
Datureae
Datura
Nicandreae
Exodeconus
Nicandra
Nolaneae
Nolana
Lycieae
Grabowskia
Lycium
Capsiceae
Lycianthes
Physaleae
Acnistus
Physalis
Nicotianoideae
Nicotiana
Petunioideae
Leptoglossis
Cestroideae
Cestrum
Browallia
Reyesia
Salpiglossis
Schizanthoideae
Schizanthus

Figure 3. A simplified tree, adapted from a cladogram, to illustrate the representation of Solanaceae subfamilies, tribes, and genera recorded from within the *lomas* formations. Adapted from Olmstead et al. (1999).

stated (p. 50), "*Schizanthus* was emerging from the north part of present Chile, and extending south and to the Andes, finally reaching Argentina." An alternative hypothesis is that the white-flowered clade (i.e., *S. integrifolius*, *S. lacteus*, and *S. candidus*) in northern Chile are allodisjuncts from the more southern species, *S. pinnatus*, and they have radiated into an unfilled niche in the north. The other *lomas* species, *S. laetus*, may be an allodisjunct of independent origin from ancestral stock not unlike *S. porrigens* or *S. tricolor*, both species restricted to central Chile (ca. 32°–33°S) with lavender flowers and bee pollination. Allodisjunctions of endemic Atacama Desert species derived from more southern Chilean congeners have been suggested in other families (Dillon & Muñoz-Schick, 1993; Gengler-Nowak, 2002). These two evolutionary hypotheses should be tested with other data.

CESTROIDEAE

The Cestroideae are represented in the *lomas* flora by three tribes and the following genera: Browallieae (*Browallia*), Cestreae (*Cestrum*), and Salpiglossideae (*Reyesia* and *Salpiglossis*). The Browallieae are a minor element in the *lomas* formations with a single autodisjunct species, *Browallia americana*, likely derived from the Andean Cordillera where all other South American taxa are confined. The Cestreae are also a minor element with *Cestrum* represented by two widely distributed, apparently autodisjunct species from the Andean Cordillera: one from central Peru, *C. auriculatum*, and another in northern Chile, *C. parqui*. The Salpiglossideae contain two, primarily Chilean genera, *Salpiglossis* and *Reyesia*. *Salpiglossis* contains two taxa, *S. spinescens*, an Atacama Desert endemic species here considered an allodisjunct from stock similar to *S. sinuata*, the other species found in the Andean Cordillera of central Chile and adjacent Argentina (30°–40°S). *Reyesia* contains four taxa, two of which are endemic species in the *lomas* formations of northern Chile: *R. chilensis* and *R. cactorum*. These two species appear to be morphologically most similar to each other and may represent allodisjunctions from ancestral stock similar to *R. parviflora*, a species of central Chile and adjacent Argentina.

NICOTIANOIDEAE

The Nicotianoideae are represented in the *lomas* formations by *Nicotiana* (tribe Nicotianeae), a genus of perhaps 95 species from North and South America and Australia with a center of diversity in the Andean Cordillera. Five species have been recorded from the *lomas* formations. These display two types of distributional patterns: autodisjuncts, such as *N. glauca*, *N. glutinosa*, and *N. paniculata* that have wider distributions in the Andean Cordillera, and allodisjunctions such as *N. knightiana* in Peru and *N. solanifolia* in Chile, both endemic species confined to a few sites. Goodspeed (1954) discussed the relationships of *Nicotiana* and suggested that most *lomas* species (*N. glauca*, *N. knightiana*, *N. paniculata*, and *N. solanifolia*) be placed in *Nicotiana* subg. *Rustica* sect. *Paniculatae* based upon tubular or salverform corollas and unwinged leaf petioles. The remaining *lomas* taxon, *N. glutinosa*, was placed in *Nicotiana* subg. *Tabacum* sect. *Tomentosae*, based upon infundibular corollas with expanded throats and winged leaf petioles. Olmstead and Palmer (1991) investigated *Nicotiana* with cpDNA restriction site analysis that included all the species found in the *lomas* formations with the exception of *N. solanifolia*. Their analysis presented a phylogeny with a well-supported, but largely unresolved clade containing *N. glutinosa*, *N. knightiana*, and *N. paniculata*. Goodspeed (1954: 341) has suggested that *N. knightiana* is "a vestige of a series of forms which once connected *N. paniculata* with *N. solanifolia* or a derivative of a hybrid between those two species."

Knapp et al. (2004) utilized nuclear and plastid genomes to test Goodspeed's sectional groupings and confirmed the placement of *Nicotiana glauca* in section *Noctiflorae* Goodsp., *N. glutinosa* in section *Undulatae* Goodsp., and *N. solanifolia*, *N. knightiana,* and *N. paniculata* in section *Paniculatae* Goodsp. It may be hypothesized that *Nicotiana* species reached the *lomas* via independent evolutionary routes and consequently at different times.

PETUNIOIDEAE

The Petunioideae are represented in the *lomas* formations by *Leptoglossis*, a genus of seven species, four of which are Peruvian endemic species. Three species, *L. darcyana*, *L. ferreyraei*, and *L. lomana*, are allodisjuncts, and *L. schwenkioides* is widespread in the Andean Cordillera and is likely an autodisjunct from upland populations. Hunziker and Sublis (1979a) considered *Leptoglossis* to be closely related to *Hunzikera*, a disjunction from the southern United States, Mexico, and Venezuela. While *Leptoglossis* has not been included in any molecular phylogenetic studies, *Hunzikeria* has been assigned to the Petunioideae by Olmstead et al. (1999) and it is placed in that subfamily here based upon the strong morphological relationship between these two genera (Hunziker, 2001). It should be mentioned that Hunziker and Sublis (1979b) considered *Salpiglossis* closely related to *Leptoglossis*, and recently Hunziker (2001) placed it in tribe Nicotianeae subtribe Leptoglossinae. The classification and relationships of *Leptoglossis* remain controversial.

SOLANOIDEAE

The Solanoideae are represented within the *lomas* formations by seven tribes: Capsiceae, Datureae, Lycieae, Nicandreae, Nolaneae, Physaleae, and Solaneae. The Capsiceae have a single widespread species, *Lycianthes lycioides*, which appears to be an autodisjunction from the adjacent Andean Cordillera. It is noteworthy, however, that the coastal populations in northern Peru possess white corollas (Fig. 2D), a floral color different from that found in the nearby Andean populations. The Datureae are represented by *Datura inoxia*, a weedy species originally from Mexico, but spread throughout South America (Jiao et al., 2002). In the *lomas* formations, this species is considered an example of an autodisjunction.

The Lycieae contain three Neotropical genera: *Grabowskia*, *Lycium*, and *Phrodus* (Hunziker & Bernardello, 1995; Hunziker, 2001). The sister-group relationship of the former two genera was supported by cpDNA data (Olmstead & Palmer, 1992; Olmstead et al., 1999). *Phrodus* is a monotypic, Chilean genus that only reaches the most southern boundary of the Atacama Desert, and it has not been recorded from the *lomas* formations (Hunziker, 2001). *Grabowskia* contains six species, primarily distributed in South America and with one species each in Chile and Peru. The Peruvian species, *G. boerhaaviaefolia*, is here considered an autodisjunct derived from populations in the Andean Cordillera, whereas the Chilean species, *G. glauca*, is a narrow endemic and considered here as an allodisjunct from congeneric stock in Argentina. *Lycium* has several species distributed in the *lomas* formations of both Chile and Peru, and their distributions suggest a combination of allopatrically derived endemic species and autodisjunctions from species found in the adjacent Andean Cordillera. Bernardello (1986) placed *lomas* species in two sections, *Lycium* sect. *Lycium* and *Lycium* sect. *Mesocope*, based upon the presence of an inconspicuous green nectary or a conspicuously red nectary, respectively. Two recent molecular systematic studies (Fukuda et al., 2001; Miller, 2002) have been completed; however, they contained only one species found in the *lomas* formations. Miller (2002) suggested that the sections of *Lycium* proposed by Bernardello (1986) were not supported by molecular data. Further, Miller's sequence and morphological analysis nested *Grabowskia* within *Lycium*, and suggested that *Grabowskia* species may comprise a clade of very divergent *Lycium*.

The Nicandreae contain two Neotropical genera: *Exodeconus* and *Nicandra.* The sister-group relationship of these two genera was supported by cpDNA data (Olmstead & Palmer, 1992; Olmstead et al., 1999), and they occupied a basal position to the rest of the subfamily Solanoideae. Two *Exodeconus* species are found in the Peruvian *lomas* formations: *E. maritimus* (Fig. 2B) in northern and central Peru, and reaching southern Ecuador, and *E. prostratus* (Fig. 2C), an endemic to the *lomas* formations. *Nicandra physalodes* (Fig. 2E) is thought to have originated in Peru; however, it is widely dispersed in tropical and subtropical areas in both the Old and New World. In Peru, this species appears to be an autodisjunction from the Andean Cordillera and is restricted to a few northern Peruvian coastal sites.

The Nolaneae are here considered monotypic, with *Nolana* as the only genus, and an undisputable member of the Solanaceae (Olmstead et al., 1999; Tago & Dillon, 1999). With its inclusion in the Solanaceae, *Nolana*, with 85 total species, becomes the fifth largest genus in the family behind *Solanum*, *Lycianthes*, *Cestrum*, and *Nicotiana* (D'Arcy, 1991). Vegetative and floral morphology are not aberrant within the Solanaceae, though the unusual ovary formed from mericarps (Fig. 2F) is unique for the Solanaceae. Mesa (1986) proposed recognizing *Nolana* as a separate family with perhaps 18 species, but D'Arcy (1991) accepted *Nolana* in the Solanaceae at the subfamilial level, Nolanoideae, and recognized 22 species in two genera, *Alona* and *Nolana.* Later, Mesa (1997; Mesa et al., 1998) revised his species concept to accept ca. 70 species. Preliminary molecular data (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994) supported observations made by previous taxonomists (Johnston, 1936) that *Nolana* shares relationships with *Lycium* and *Grabowskia.* The placement of *Nolana* within the Solanaceae changes the diagnosis of the family, adding mericarps to the possible fruit types, and Olmstead and Palmer (1992) consequently suggested that undue emphasis had been placed upon the gynoecium morphology in defining taxonomic groups. *Nolana* exhibits extensive variation in habit, ecological preferences, and vegetative and floral morphology with both showy flowers, e.g., *Nolana rupicola* (Fig. 2G), and reduced forms, e.g., *Nolana peruviana* (Fig. 2H). Additional *Nolana* corollas may be observed via the internet <http://www.sacha.org/Nolana/corollas. htm>.

Species diversity in *Nolana* is nearly equally divided between Chile and Peru. At least one species of *Nolana* occurs in every *lomas* formation throughout Peru and Chile, and at some locations as many as 10 species occur sympatrically. There are 37 endemic species recorded from Peru (4 in Sector 1 and 37 in Sector 2), another 42 endemic species recorded from Chile (Sector 3), four species are found in both southern Peru and northern Chile, and one species is an endemic to the Galápagos Islands, Ecuador. No fewer than 70 species are considered to be endemic to the *lomas* formations of Chile and Peru in about equal numbers. Another 13 species occur in upland habitats (> 1000 m) outside of the area normally included in the *lomas* formations (<http://www.sacha.org/famil/nolana/Nolana_sectoring.htm>). One species, *N. paradoxa*, has an extended distributional range from central Chile to southern coastal Chile (33°S–42°30′S).

Tago (1999) analyzed ITS and *mat*K to estimate phylogenetic relationships within a sampling of 37 species of *Nolana*, including members from both Chile and Peru and two outgroup species, *Atropa belladonna* L. and *Grabowskia glauca* Schltdl. The preliminary data provided conflicting hypotheses of relationships with results largely incongruent between *mat*K and ITS studies (Tago & Dillon, 1999). Further investigations are under way, and data from six molecular data sets including the nuclear ITS regions, 5S spacer, and GBSSI gene, and the chloroplast *trn*C-*trn*D region and *ndh*F gene have been accessed. There appears to be a strong biogeographic signal in preliminary data indicating a deep split between the *Nolana* species from Peru and Chile (J. Wen, pers. comm.), and this pattern is also reflected in the overall flora of these deserts (see FLORISTIC STUDY). As no other element within the flora, the evolutionary history of *Nolana* holds clues to the age and origin of the coastal deserts and their unique flora.

The Physaleae are represented by two tribes and genera: Iochrominae (*Acnistus*) and Physalinae (*Physalis*). *Acnistus* is a Neotropical, monotypic genus common from Mexico to Brazil, and the occurrence of *Acnistus arborescens* in the *lomas* formations is here considered an example of an autodisjunct from the Andean Cordillera populations. *Physalis* has two widely distributed species with rare occurrences within the *lomas* formations; both *P. angulata* and *P. peruviana* are considered to be cases of autodisjunct distributions from nearby Andean Cordillera populations.

The Solaneae are represented by *Jaltomata* and *Solanum* including *Lycopersicon*. These two genera have species within the *lomas* formations considered as autodisjuncts from nearby Andean Cordillera species and allodisjuncts confined to the *lomas* formations. Molecular systematic studies have placed *Jaltomata* as basal to *Solanum*, and *Lycopersicon* grouped with *Solanum* species (Bohs & Olmstead, 1999; Olmstead & Palmer, 1992; Olmstead et al., 1999).

Jaltomata is under systematic study (Mione et al., 2000a, 2000b), but the relationships among its four species found in the Peruvian *lomas* formations have not been elucidated. *Jaltomata aspera* likely represents an autodisjunction from adjacent Andean Cordillera; however, it is possible that the population in *lomas* formations represents a distinct, endemic species (T. Mione, pers. comm.). The other three species, *J. hunzikeri*, *J. lomana*, and *J. umbellata*, are considered allodisjuncts and hypothesized to have been derived from ancestral stock from the adjacent Andean Cordillera. They may either have radiated from an initial introduction, in which case they would be expected to be more closely related to each other, or they may each represent independent introductions (Mione et al., 1994).

Solanum has 21 species within the *lomas* formations of Chile and Peru: 16 placed in subgenus *Solanum* and 5 species in section *Lycopersicon* (Peralta & Spooner, 2000, 2001). Molecular phylogenies (Olmstead & Palmer, 1992; Peralta & Spooner, 2001) reveal that *Lycopersicon* is not distinct from *Solanum* (Bohs & Olmstead, 1999), though its placement in *Solanum* is controversial and has not been accepted by all authors (Hunziker, 2001; Nee, 1999). The *lomas* species are all classified as *Solanum* sect. *Lycopersicon* subsect. *Lycopersicon*. In the phylogenetic analysis of the GBSSI gene sequences, Peralta and Spooner (2001) suggested that *S. pennellii* and *S. habrochaites* are a well-supported clade in the basal polytomy. *Solanum peruvianum* is considered paraphyletic and separates into two geographical groups, one in northern Peru (e.g., Cerro Campana, 7°58′S) and the other in central Peru (Dept. Ancash, 9°55′S), southern Peru (Dept. Arequipa, 17°02′S), and northern Chile (Prov. Tarapaca, 18°28′S). Further, they found that

Solanum pimpinellifolium was most closely related to *Solanum lycopersicum* (the cultivated tomato). Sacks et al. (1997) speculated that montane races of *S. peruvianum* (as *Lycopersicon peruvianus*) could be derived from coastal races and may form natural hybrids with *S. chilense* (as *Lycopersicon chilensis*) where their ranges overlap in southern Peru. The close relationship between these species invites speculation as to the timing of the arrival of each to the coastal environments. A vicariant origin of the *S. peruvianum* and *S. chilense* should be tested, certainly, and the origins of species with distributions within the *lomas* formations merits further investigation (Spooner et al., 2005).

The remaining 16 species are classified in *Solanum* subg. *Solanum* and display both autodisjunct and allodisjunct distributional patterns. Two species found in the *lomas* formations are considered autodisjunctions: *Solanum radicans* (sect. *Dulcamara*), distributed widely in South America, and *S. fragile* (sect. *Solanum*); both species are found at higher elevations in the Andean Cordillera of southern Peru. The remaining *Solanum* species are grouped into two sections, *Solanum* sect. *Regmandra* (Nee, 1999), which contains seven species, here considered allodisjuncts and confined to the *lomas* formations: *S. brachyantherum* (Chile), *S. ferreyrae* (southern Peru), *S. montanum* (Peru), *S. multifidum* (Peru), *S. murphyi* (southern Peru), *S. phyllanthum* (Chile and Peru), and *S. remyanum* (Chile). And the second, *Solanum* sect. *Petota* ser. *Tuberosa* (Nee, 1999), a suite of seven strictly Peruvian species: *S. chancayense*, *S. immite*, *S. medians*, *S. mochiquense*, *S. neoweberbaueri*, *S. tuberosum*, and *S. wittmackii*. The relationships of the second group of species have not been investigated, but most have distributions outside of the *lomas* formations and may be considered as autodisjunctions. The presence of *Solanum tuberosum* (cultivated potato) in the *lomas* formations may be attributed to human activities, since potatoes are cultivated in some coastal sites during El Niño events when sufficient moisture is available (pers. obs.).

DISCUSSION

The biogeographic patterns of the Solanaceae in the *lomas* formations of Chile and Peru reflect independent histories for various subfamilies, tribes, genera, and species, and it may be hypothesized that some members are long-time occupants of the deserts and others are potentially more recent introductions. Thirteen of 18 genera with *lomas* representatives are considered to be Neotropical in their overall distribution. Five subfamilies are represented in the *lomas* formations (Fig. 3) and each contains endemic species distributed among the following nine genera: *Exodeconus* (1 sp.), *Grabowskia* (1 sp.), *Jaltomata* (3 spp.), *Leptoglossis* (3 spp.), *Nolana* (70 spp.), *Reyesia* (2 spp.), *Salpiglossis* (1 sp.), *Schizanthus* (4 spp.), and *Solanum* (7 spp.). Of the 128 species recorded for the Solanaceae in the *lomas* formations, 90 species are considered endemic to these environments (70%). Endemism is equally divided between Chile and Peru, with an estimated 43 Chilean endemic species and 45 Peruvian endemic species. Of the total number of Solanaceae species reported from the *lomas* flora, only nine are recorded from both Chile and Peru, i.e., *Nolana* (4 spp.), *Solanum* (3 spp.), *Lycium* (1 sp.), and *Nicotiana* 1 (sp.). Of these, all four *Nolana* species and two *Solanum* species are considered *lomas* endemics as well. It is considered that the species that are endemic in the *lomas* formations represent allodisjuncts from ancestral, congeneric stocks now extinct, either derived from the proximal Andean Cordillera of Peru or semi-arid habitats in central Chile. Some 38 species may be considered examples of autodisjuncts most often originating from extant, conspecific populations in the adjacent Andean Cordillera in either Peru or Chile. There is a suite of 12 species in the northern Peruvian *lomas* formations (7°–13°S) in several genera that are all considered to be autodisjunctions with direct connections to nearby conspecific Andean populations. Without appropriate data, it cannot be determined with certainty which species are potentially original *lomas* dwellers that have dispersed into upland habitats within the Andean Cordillera.

The Solanaceae subfamily Schizanthoideae and subfamily Cestroideae tribe Salpiglossideae are primarily Chilean and adjacent Argentinean in distribution, with a number of endemic species reaching the *lomas* formations of the northern Atacama Desert. Solanaceae subfamily Cestroideae tribe Browallieae and subfamily Solanoideae tribes Datureae and Physaleae are prevalent in both North and South America and reach the northern and central Andean Cordillera of Peru. Solanaceae subfamily Petunioideae is primarily a Central and South American group, and *Leptoglossis* has four of its five taxa as endemic species confined to the *lomas* formations of Peru, and with one autodisjunct species in Argentina, a pattern found in other southern Peruvian taxa, e.g., *Bulnesia retama*, Zygophyllaceae (Solbrig, 1976). It has been suggested (Hunziker & Sublis, 1979a) that *Leptoglossis* shares relationships with *Hunzikeria*, an amphitropic disjunction from the southern United States, Mexico, and Venezuela. That these two taxa represent the product of an amphitropic disjunction is an interesting hypothesis that should be tested.

Allodisjuncts represented by endemic Peruvian *lomas* species are found in Solanaceae subfamily Solanoideae tribe Solaneae (*Jaltomata*, *Solanum*), Nicandreae (*Exodeconus*), and Nolaneae (*Nolana*). Allodisjuncts represented by endemic Chilean *lomas* species are found in Solanaceae subfamily Solanoideae tribes Lycieae (*Grabowskia*, *Lycium*) and Nolaneae (*Nolana*), and in each of these genera the most closely related species are distributed in habitats immediately south of the Atacama Desert in central to southern Chile and/or adjacent Argentina. As treated here, *Nolana* is considered to have 85 total species, and of these, 70 are restricted to the *lomas* formations, with approximately equal numbers of endemic species in Chile and Peru.

Olmstead and Palmer (1992) dated the early diversification of the Solanaceae at ca. 50 million years ago or early Eocene. The first appearance of *Nolana* was estimated using *mat*K (Tago, 1999) or *rbc*L sequences (Olmstead & Sweere, 1994) as middle Miocene (10–11 mya). The constituents of the Solanaceae within the *lomas* formations represent a complex picture with multiple sources and origins for representative genera and species. These taxa offer many interesting examples of types and timing of disjunctions, including autojuncts and allodisjuncts formed via dispersal and subsequent modification (i.e., founder effects) or through vicariant events. Much remains to be accomplished in our search for modes of evolution and speciation in the *lomas* formations and the interplay of distributions with climatic, geological history, and potential vicariant events.

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APPENDIX I

The following is an annotated list of the species of Solanaceae encountered in the *lomas* formations in the coastal deserts of Chile and Peru. The subfamilial, tribal, and subtribal classification follows that proposed by Olmstead et al. (1999). Publication citations for each species, generic, specific and *lomas* formation distributions, relevant literature, and a voucher for each species are provided. Whenever possible, collections made by the author are cited and these have or will have duplicates distributed in appropriate South American herbaria. Additional vouchers may be found in the LOMAFLOR database posted on the internet <http://www.sacha.org/>.

1. *Acnistus* Schott.

Solanoideae, Physaleae, Iochrominae

Generic distribution. *Acnistus* is a Neotropical, shrubby genus of one or perhaps two species distributed from Mexico, Central America, and the Caribbean to Andean South America, Galápagos Islands, and Brazil. The genus has been interpreted as monotypic by Hunziker.

Literature. D'Arcy (1991), Hunziker (1960, 1982, 2001), Macbride (1962).

1.1. *Acnistus arborescens* (L.) Schltdl., Linnaea 7: 67. 1832.

Species distribution. This species is a native to northwestern South America. In Peru, it is found in the northeastern Andes and has been recorded from the *lomas* formations of Dept. La Libertad (Cerro Campana) and Dept. Lima (Lachay, Atocongo, Pachacamac, Manzano).

Voucher. *Knapp 8309* (F).

2. *Browallia* L.

Cestroideae, Browallieae

Generic distribution. *Browallia* is a Neotropical genus of two to seven species, distributed from the southern United States, Mexico, Central America, Antilles, and throughout the Andean Cordillera from Colombia to Bolivia. The genus occupies a wide range of environments, and the number of species accepted in the genus has varied greatly between seven species accepted by Dios, to four by Brako and Zarucchi, three by D'Arcy, and two by Hunziker.

Literature. Brako & Zarucchi (1993), D'Arcy (1991), Dios (1977), Hunziker (1995), Leiva-G. (1995), Macbride (1962), Sagástegui & Dios (1980).

2.1. *Browallia americana* L., Sp. Pl. 1: 631. 1753.

Species distribution. This species ranges widely in tropical America from Mexico to Peru and the Galápagos Islands. It is found in Andean locales from northern to central Peru and recorded from coastal *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Chipitur, Virú), Dept. Ancash (Lupín), and Dept. Lima (Amancaes, Asia, and Quilmaná).

Voucher. *Dillon & Santisteban 4713* (F).

3. *Cestrum* L.

Cestroideae, Cestreae

Generic distribution. *Cestrum* is a woody genus of ca. 250 species distributed primarily in tropical America with ca. 150 species from South America. There are two species recorded from the *lomas* formations, one each in Chile and Peru.

Literature. Francey (1935,1936), Macbride (1962), Matthei (1995).

3.1. *Cestrum auriculatum* L'Hérit., Stirp. Nov. 73, t. 35. 1788.

Species distribution. This species is widespread throughout Andean Ecuador and Peru, but rare within the *lomas* formations of Dept. Lima (Manzano, Pachacamac, Asia, Lurín) and Ica (Chincha Alto).

Voucher. *Knapp 8333* (F).

3.2. *Cestrum parqui* L'Hérit., Stirp. Nov. 73, t. 36. 1788.

Species distribution. This species is widespread throughout southern South America from Brazil, Uruguay, Argentina, and Chile. Only one collection is recorded from the *lomas* formations of coastal Chile of Prov. Antofagasta (Miguel Díaz).

Voucher. *Dillon et al. 8080* (F).

4. *Datura* L.

Solanoideae, Datureae

Generic distribution. *Datura* is a Neotropical genus of 8 to 10 annual species distributed from the southwestern United States, Mexico, Central America, and the Caribbean and introduced to the Galápagos Islands, Andean South America, Brazil, and Asia.

Literature. Avery et al. (1959), D'Arcy (1991), Macbride (1962), Persson et al. (1999), Symon & Haegi (1991).

4.1. *Datura inoxia* Mill., Gard. Dict. ed. 8, no. 5. 1768.

Species distribution. This species is distributed from Mexico, Central America, and South America from Venezuela to Paraguay. In Peru, it is considered an introduced herb and is rare within the *lomas* formations with only one collection record from Dept. Arequipa (Atiquipa).

Voucher. *Ochoa & Salas 14903* (F).

5. *Exodeconus* Raf.

Solanoideae, Nicandreae

Generic distribution. *Exodeconus* is a Neotropical genus of six annual species distributed in northern Chile, Ecuador (mainland and Galápagos Islands), and coastal Peru. Though the genus does occur at high elevations in Chile, its species do not reach the coastal *lomas* formations.

Literature. Axelius (1994), Barboza et al. (1997).

5.1. *Exodeconus maritimus* (Benth.) D'Arcy, Solanaceae Newsl. 2(4): 19. 1986.

Species distribution. A species from near-ocean to upland Andean sites, ranging from northern to central Peru and one record from southern Ecuador. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana, Cerro Cabezón, Virú), Dept. Ancash (Huarmey), Dept. Lima, and Dept. Nasca.

Voucher. *Dillon & Whalen 4005* (F).

5.2. *Exodeconus prostratus* (L'Hérit.) Raf., Sylva Tellur. 57. 1838.

Species distribution. A Peruvian species endemic to coastal *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Virú), Dept. Ancash (Lupín), and Dept. Lima (Lachay, San Gerónimo, San Bartolomé, Amancaes, San Agustín).

Voucher. *Dillon & Santisteban 4697* (F).

6. *Grabowskia* Schltdl.

Solanoideae, Lycieae

Generic distribution. *Grabowskia* is a Neotropical, shrubby genus of ca. six species native to temperate South America with a disjunct of one species to Mexico (D'Arcy, 1991). There are two species recorded from the *lomas* formations, one each from Chile and Peru.

Literature. Bernardello (1982), Hunziker (1979).

6.1. *Grabowskia boerhaaviaefolia* (L.f.) Schltdl., Linnaea 7: 71. 1832.

Species distribution. A species of lower elevations and arid sites in Peru and the Galápagos Islands. It is recorded from northern Peruvian *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Chiputur, Cerro Negro, Virú).

Voucher. *Leiva & Dillon 2191* (F).

6.2. *Grabowskia glauca* (Phil.) I. M. Johnst., Contr. Gray Herb. 85: 112. 1929.

Species distribution. A Chilean species endemic to the *lomas* formations in two geographically adjacent populations of Prov. Antofagasta (Hueso Parado, Quebrada San Ramón).

Voucher. *Dillon & Teillier 5194* (F).

7. *Jaltomata* Schltdl.

Solanoideae, Solaneae

Generic distribution. *Jaltomata* is a Neotropical genus of about 45 species of herbs or shrubs distributed from the southwestern United States, Mexico, Central America, and Greater Antilles to Andean South America as far south as Bolivia; one species is disjunct in the Galápagos Islands. Four species are currently recorded from coastal Peru.

Literature. Gentry (1973), Mione (1999), Mione & Coe (1992), Mione et al. (1993, 2000a, 2000b).

7.1. *Jaltomata aspera* (Ruiz & Pav.) Mione, Novon 2: 383. 1992.

Species distribution. A Peruvian species recorded in near-coastal Andean habitats from central and southern Peru. In the *lomas* formations, it is recorded from sites in Dept. Lima (Atocongo, Amancaes, San Gerónimo) and Dept. Arequipa (Atiquipa).

Voucher. *Macbride 5912* (F).

7.2. *Jaltomata hunzikeri* Mione, Rhodora 102: 385. 2000.

Species distribution. A Peruvian species endemic to a single *lomas* formation from Dept. Lima (Pativilca).

Voucher. *Stork et al. 9228* (GH).

7.3. *Jaltomata lomana* Mione & S. Leiva, Novon 10: 54. 2000.

Species distribution. A Peruvian species endemic to a single *lomas* formation from Dept. Ancash (Mongon).

Voucher. *Leiva et al. 2140* (F).

7.4. *Jaltomata umbellata* (Ruiz & Pav.) Mione & M. Nee, Brittonia 45: 144. 1993.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Lima (Lachay, Atocongo, San Agustín).

Voucher. *Dillon et al. 3626* (F).

8. *Leptoglossis* Benth.

Petunioideae, Leptoglossinae

Generic distribution. *Leptoglossis* is a Neotropical genus of seven annual to perennial species, mostly Peruvian in distribution, but with one disjunct endemic species in Argentina. Four species are known from the *lomas* formations of coastal Peru.

Literature. Hunziker & Subils (1979a, 1979b).

8.1. *Leptoglossis darcyana* Hunz. & Subils, Lorentzia 3: 15. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Atico) and Dept. Tacna (Sama Grande, Tacna).

Voucher. *Dillon & Dillon 3895* (F).

8.2. *Leptoglossis ferreyraei* Hunz. & Subils, Bot. Mus. Leafl. 27: 16. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Jahuay, Atiquipa, Pongo).

Voucher. *Dillon et al. 8198* (F).

8.3. *Leptoglossis lomana* (Diels) Hunz., Bot. Mus. Leafl. 27: 18. 1979.

Species distribution. A Peruvian species endemic to *lomas* formations from Dept. Arequipa (Camaná, Capac, Mejía).

Voucher. *Hutchison 1298* (F).

8.4 *Leptoglossis schwenkioides* Benth., Bot. Voy. Sulphur 143. 1845.

Species distribution. A Peruvian species found throughout the northern Andean Cordillera and coastal *lomas* formations from Dept. La Libertad (Cerro Chiputur), Dept. Lima (Cajamarquilla).

Voucher. *Hutchison 1032* (F).

9. *Lycianthes* (Dunal) Hassler.

Solanoideae, Capsiceae

Generic distribution. *Lycianthes* is a Neotropical, shrubby genus of ca. 200 species distributed from East Asia and South America. A single widespread species is reported from the *lomas* of northern Peru.

9.1. *Lycianthes lycioides* (L.) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 181. 1917.

Species distribution. A species widespread throughout South America from Venezuela to Argentina, and common in Andean Peru. In the coastal *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana, Cerro Chiputur, Cerro Cabras, Virú).

Voucher. *Dillon et al. 2701* (F).

10. *Lycium* L.

Solanoideae, Lycieae

Generic distribution. *Lycium* is a cosmopolitan genus of shrubs and subshrubs with ca. 80 species distributed throughout tropical and extra-tropical North and South America and the Galápagos Islands. In the coastal ***lomas*** formations, five species are recorded from Peru and Chile.

Literature. Bernardello (1986).

10.1. *Lycium americanum* Jacq., Select. Stirp. Amer. Hist.: 50. 1763.

Species distribution. A widespread species found throughout the Caribbean and South America. In Peru, it is widespread in both the Andean Cordillera and in *lomas* formations from Dept. La Libertad (Cerro Campana) and Dept. Lima (San Agustín, Cañete, Lurín).

Voucher. *Weberbauer 5226* (F).

10.2. *Lycium deserti* Phil., Fl. Atacam. 43. 1860.

Species distribution. A Chilean species recorded from high-elevation localities and **lomas** formations from Prov. Antofagasta (Paposo, Hueso Parado) and Prov. Atacama (Pan de Azúcar).

Voucher. *Dillon et al. 5555* (F).

10.3. *Lycium distichum* Meyen, Reise 1: 448. 1834.

Species distribution. A species recorded from high-elevation localities in southern Peru and northern Chile. Bernardello listed the voucher cited here, a Peruvian collection from Dept. Arequipa (Mollendo).

Voucher. *Gourlay 133* (K).

10.4. *Lycium leiostemum* Wedd., Chlor. Andina 2: 108. 1850.

Species distribution. A species recorded from the Andean Cordillera of Peru and from several *lomas* formations in northern Chile from Prov. Tarapacá (Iquique) and Prov. Antofagasta (Cerro Moreno, La Chimba, Quebrada El Rincón, Cifuncho, Quebrada Cachina).

Voucher. *Pinto s.n.* (SGO #143002).

10.5. *Lycium stenophyllum* Remy, in Gay, Flora Chilena 5: 94. 1849.

Species distribution. A species recorded from southern Peru and northern Chile. It is known from *lomas* formations from Peru, Dept. Arequipa (Mollendo), and Chile, Prov. Antofagasta (Cobija) and Prov. Atacama (Copiapó).

Voucher. *Dillon & Dillon 3961* (F).

11. *Nicandra* Adans.

Solanoideae, Nicandreae

Generic distribution. *Nicandra* is a monotypic genus thought to have originated in Peru but now widely distributed and weedy in tropical and subtropical regions around the world.

Literature. Hunziker (1979), Macbride (1962).

11.1. *Nicandra physalodes* (L.) Gaertn., Fruct. 2: 237, pl. 131, fig. 2. 1791.

Species distribution. A species recorded from throughout the Andean Cordillera of Peru, and reaching *lomas* formations from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Chiputur, Virú) and Dept. Lima (Lurín). It is cultivated in Chile, but has not been recorded from the *lomas* formations in that country.

Voucher. *Dillon et al. 2707* (F).

12. *Nicotiana* L.

Nicotianoideae, Nicotianeae

Generic distribution. *Nicotiana* is a genus of about 95 species primarily distributed in South America, Australia, and the islands of the South Pacific. Peru has 15 species recorded from throughout the Andean Cordillera, and Chile has 13 species in central and southern regions. Most species are small to large herbs but a few are shrubby. Five species are represented in the lomas formations, two recorded from Chile and four from Peru.

Literature. Goodspeed (1954).

12.1. *Nicotiana glauca* Graham, Edinburgh New Philos. J. 5: 175. 1828.

Species distribution. A species native to Argentina, but worldwide in distribution. It is recorded from *lomas* formations from Peru, Dept. Arequipa (Mollendo) and Dept. Tacna (Sama Grande), and Chile, Prov. Atacama (Vallenar).

Voucher. *Ferreyra 12074* (F).

12.2 *Nicotiana glutinosa* L., Sp. Pl. 1: 181. 1753.

Species distribution. A species found throughout the Andean Cordillera of Peru and the Galápagos Islands. It is recorded from *lomas* formations of northern Peru, Dept. La Libertad (Cerro Cabezón, Virú).

Voucher. *Sagástegui & López 10985* (F).

12.3. *Nicotiana knightiana* Goodspeed, Univ. Calif. Publ. Bot. 18: 139. 1938.

Species distribution. A Peruvian species endemic to the *lomas* formations from Dept. Arequipa (Mollendo).

Voucher. *Worth & Morrison 15696* (UC).

12.4 *Nicotiana paniculata* L., Sp. Pl. 1: 180. 1753.

Species distribution. A Peruvian species from the Andean Cordillera and the *lomas* formations from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Chipitur, Virú), Dept. Ancash (Casma, Lupín), Dept. Lima (Lachay, Manzano, Atocongo, Quilmaná), and Dept. Arequipa (Capárra, Mejía).

Voucher. *Dillon et al. 3634* (F).

12.5. *Nicotiana solanifolia* Walp., Repert. Bot. Syst. 3: 12. 1844–1845.

Species distribution. A Chilean species endemic to *lomas* formations from Prov. Antofagasta (Miguel Díaz, Paposo, Hueso Parado, Taltal) and Prov. Atacama (Chañaral).

Voucher. *Dillon et al. 5741* (F).

13. *Nolana* L.f.

Solanoideae, Nolaneae

Generic distribution. *Nolana* is a Neotropical genus distributed from northern Peru to southern Chile and one disjunct, endemic species in the Galápagos Islands (Tago & Dillon, 1999). Most of its ca. 85 species are confined to the *lomas* formations where 70 species are recorded from Peru and Chile. A few range into higher elevation sites in Peru and Chile, well inland and outside of the influence of coastal fogs. Four *Nolana* species have distributions crossing from southern Peru to northern Chile: *N. adansonii, N. gracillima, N. lycioides, and N. jaffuelii.* All other species are confined to either Chile or Peru, and most have narrow distributions.

Literature. Ferreyra (1961, 1974), Johnston (1936), Mesa (1981, 1986, 1997), Mesa et al. (1998), Tago & Dillon (1999).

13.1. *Nolana acuminata* (Miers) Miers ex Dunal, Prodr. 13: 12. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations from Prov. Antofagasta to Prov. Valparaíso.

Voucher. *Dillon 8100* (F).

13.2. *Nolana adansonii* (Roem. & Schult.) I. M. Johnst., Contr. Gray Herb. 112: 47. 1936.

Species distribution. An endemic species found in the *lomas* formations of southern Peru, Dept. Arequipa (Atico, Atiquipa), and one disjunct population in northern Chile, Prov. Tarapacá (Iquique).

Voucher. *Dillon & Dillon 3744* (F).

13.3. *Nolana albescens* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 66. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (La Cachina) and Prov. Atacama (Caldera, Bahia Inglesa, Copiapó).

Voucher. *Dillon & Dillon 6040* (F).

13.4. *Nolana amplexicaulis* Ferreyra, Publ. Mus. Nat. Hist. "Javier Prado", Ser. B. 10: 7. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Capac).

Voucher. *Ferreyra 11747* (USM).

13.5. *Nolana aplocaryoides* (Gaudich.) I. M. Johnst., Contr. Gray Herb. 112: 57. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Salar del Carmen, Caleta Botija, Paposo, Taltal, Hueso Parado; Tortolas), and Prov. Atacama (Pan de Azúcar, Chañaral, Caleta Obispito, Caldera).

Voucher. *Dillon & Dillon 5660* (F).

13.6. *Nolana arenicola* I. M. Johnst., Contr. Gray Herb. 112: 29. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay) and Dept. Tacna (Sama Grande).

Voucher. *Dillon et al. 3284* (F).

13.7. *Nolana aticoana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 13. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico).

Voucher. *Dillon & Dillon 3838* (F).

13.8. *Nolana baccata* (Lindl.) Dunal, Prodr. 13: 14. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Caldera, Copiapó, Huasco).

Voucher. *Marticorena 1869* (CONC).

13.9. *Nolana balsamiflua* (Gaudich.) Mesa, Fl. Neotrop. 26: 68. 1981.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, Tocopilla).

Voucher. *Dillon & Dillon 5726* (F).

13.10. *Nolana carnosa* (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Caldera, Bahia Inglesia).

Voucher. Dillon & Trujillo 8093 (F).

13.11. *Nolana cerrateana* Ferreyra, Publ. Mus. Nat. Hist. "Javier Prado," Ser. B. 10: 11. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico, Camaná, Mollendo, Cachendo).

Voucher. *Dillon et al. 8215* (F).

13.12. *Nolana clivicola* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, La Chimba).

Voucher. *Dillon & Dillon 5721* (F).

13.13. *Nolana coelestis* (Lindl.) Miers ex Dunal, Prodr. 13: 13. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Travesía, Huasco Bajo) and Prov. Coquimbo (La Serena).

Voucher. *Dillon et al. 5436* (F).

13.14. *Nolana confinis* I. M. Johnst., Contr. Gray Herb. 112: 78. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Nasca), Dept. Arequipa (Ocoña, Mollendo), and Dept. Tacna (Sama Grande).

Voucher. *Dillon et al. 3383* (F).

13.15. *Nolana coronata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 112b. 1799.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay, Atiquipa, Atico, Capac, Chala, Mollendo).

Voucher. *Dillon et al. 8200* (F).

13.16. *Nolana crassulifolia* Poepp., Froriep's Not. Natur-Heilk. 23: 276. 1829.

Species distribution. A Chilean species recorded in the *lomas* formations of Prov. Atacama (Carrizal Bajo), and extending to coastal sites in Prov. Coquimbo and Prov. Valparaíso (Concon).

Voucher. *Dillon et al. 5435* (F).

13.17. *Nolana deflexa* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 71. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pan de Azúcar).

Voucher. *Harding 2* (GH).

13.18. *Nolana diffusa* I. M. Johnst., Contr. Gray Herb. 112: 77. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Miguel Díaz, Hueso Parado).

Voucher. *Dillon & Dillon 5644* (F).

13.19. *Nolana divaricata* (Lindl.) I. M. Johnst., Contr. Gray Herb. 112: 64. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (La Chimba, Hueso Parado, Taltal, Bahia Tórtolas).

Voucher. *Dillon & Teillier 5339* (F).

13.20. *Nolana elegans* (Phil.) Reiche, Anales Univ. Chile 125: 487. 1910.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, La Chimba, Caleta Botija, El Rincón, Paposo, Hueso Parado, Esmeralda) and Prov. Atacama (Caleta Obispito).

Voucher. *Dillon et al. 5483* (F).

13.21. *Nolana filifolia* (Hook. & Arn.) I. M. Johnst., Revista Chilena Hist. Nat. 34: 231. 1930.

Species distribution. A Chilean species recorded from Prov. Atacama (Pan de Azúcar) and extending to Prov. Coquimbo (Buenos Aires, Huentelauquén).

Voucher. *Dillon & Teillier 4973* (F).

13.22. *Nolana flaccida* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 60. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Las Bombas, Pan de Azúcar).

Voucher. *Dillon et al. 5608* (F).

13.23. *Nolana gayana* (Gaudich.) Koch, Ind. Sem. Berol. 12. 1855.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. La Libertad (Cerro Chiputur) and Dept. Lima (Pasamayo, Atocongo).

Voucher. *Dillon et al. 4676* (F).

13.24. *Nolana glauca* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 66. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pan de Azúcar) and Prov. Coquimbo (Los Vilos).

Voucher. *Dillon & Trujillo 8019* (F).

13.25. *Nolana gracilliana* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 59. 1936.

Species distribution. A species ranging from the *lomas* formations of southern Peru, Dept. Arequipa (Arequipa), Dept. Moquegua (Moquegua), Dept. Tacna (Sama Grande) to northern Chile, Prov. Tarapacá (Arica) and Prov. Antofagasta (Tocopilla).

Voucher. *Dillon et al. 4773* (F).

13.26. *Nolana guentherii* I. M. Johnst., Contr. Gray Herb. 112: 55. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Cachendo).

Voucher. *Guenther & Buchtien 113* (GH).

13.27. *Nolana humifusa* (Gouan) I. M. Johnst., Contr. Gray Herb. 112: 50. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Cabras, Cerro Chiputur, Cerro Negro, Virú), Dept. Ancash (Casma, Lupín), and Dept. Lima (Lachay, Iguanil, Pasamayo, Amancaes, Cerro Agustino, Atocongo, Lurín).

Voucher. *Dillon et al. 4654* (F).

13.28. *Nolana incana* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 68. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Mantancilla, Bandurrias, San Ramón) and Prov. Atacama (Esmeralda, Pan de Azúcar, Caleta Obispito).

Voucher. *Dillon & Trujillo 8010* (F).

13.29. *Nolana inconspicua* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, Tocopilla, Cerro Moreno, La Chimba).

Voucher. *Teillier 457* (CONC).

13.30. *Nolana inflata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 112a. 1799.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Cháparra, Atiquipa, Atico).

Voucher. *Dillon et al. 3844* (F).

13.31. *Nolana insularis* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 49. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Isla de San Gallán).

Voucher. *Murphy 3472* (GH).

13.32. *Nolana intonsa* I. M. Johnst., Contr. Gray Herb. 112: 34. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Tarapacá (Iquique).

Voucher. *Pinto s.n.* (SGO #142968).

13.33. *Nolana ivaniana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 3. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo).

Voucher. *Dillon et al. 8219* (F).

13.34. *Nolana jaffuelii* I. M. Johnst., Contr. Gray Herb. 112: 39. 1936.

Species distribution. A species endemic to the *lomas* formations of Chile, Prov. Tarapacá (Iquique), Prov. Antofagasta (Tocopilla) and Peru, Dept. Tacna (Tacna).

Voucher. *Pinto s.n.* (SGO #142973).

13.35. *Nolana johnstonii* Vargas, Rev. Univ. (Cuzco) 107: 155. 1954.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Moquegua (Ilo).

Voucher. *Dillon et al. 8225* (F).

13.36. *Nolana latipes* I. M. Johnst., Contr. Gray Herb. 112: 30. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo, Mejía).

Voucher. *Worth 15709* (F).

13.37. *Nolana leptophylla* (Miers) I. M. Johnst., Contr. Gray Herb. 112: 73. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, El Cobre, Quebrada Médano, Taltal) and Prov. Atacama (Carrizal Bajo), and can range to interior sites above 2000 m.

Voucher. *Dillon et al. 5730* (F).

13.38. *Nolana linearifolia* Phil., Anales Univ. Chile 91: 28. 1895.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Punta Hornos, Cuesta Barriles, Cerro Moreno, La Chimba, Paposo, Quebrada San Ramón).

Voucher. *Dillon et al. 5890* (F).

13.39. *Nolana lycioides* I. M. Johnst., Contr. Gray Herb. 112: 70. 1936.

Species distribution. A species endemic to the *lomas* formations of Chile, Prov. Tarapacá (Iquique), and Peru, Dept. Moquegua (Ilo) and Dept. Tacna (Sama Grande).

Voucher. *Dillon et al. 8227* (F).

13.40. *Nolana mariarosae* Ferreyra, Bol. Soc. Peruana Bot. 7(1–2): 3. 1974.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atico, Ocoña).

Voucher. *Ferreyra 12490* (USM).

13.41. *Nolana minor* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 4. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Camaná), possibly extinct due to habitat destruction at type locality.

Voucher. *Ferreyra 2535* (USM).

13.42. *Nolana mollis* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 61. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Paposo, Taltal, Tórtolas) and Prov. Atacama (Pan de Azúcar, Copiapó).

Voucher. *Dillon & Trujillo 8015* (F).

13.43. *Nolana pallida* I. M. Johnst., Contr. Gray Herb. 112: 69. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Marcona) and Dept. Arequipa (Jahuay, Atico, Capac, Atiquipa).

Voucher. *Dillon et al. 8205* (F).

13.44. *Nolana pallidula* I. M. Johnst., Contr. Gray Herb. 112: 31. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Atiquipa, Atico, Camaná), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande, Tacna).

Voucher. *Dillon et al. 8226* (F).

13.45. *Nolana parviflora* (Phil.) Phil., Anales Univ. Chile 91: 29. 1895.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Pajonales, Caldera, Monte Amargo).

Voucher. *Werdermann 460* (GH).

13.46. *Nolana pearcei* I. M. Johnst., Contr. Gray Herb. 112: 58. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Tacna (Tacna).

Voucher. *Pearce s.n.* (BM #21199).

13.47. *Nolana peruviana* (Gaudich.) I. M. Johnst., Contr. Gray Herb. 112: 66. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Tocopilla, Cerro Moreno, La Chimba, El Cobre, Paposo), and Prov. Atacama (Carrizal Bajo).

Voucher. *Dillon & Dillon 5622* (F).

13.48. *Nolana pilosa* I. M. Johnst., Contr. Gray Herb. 112: 79. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo, Mejia, Cachendo).

Voucher. *Dillon & Dillon 3908* (F).

13.49. *Nolana platyphylla* (I. M. Johnst.) I. M. Johnst., Contr. Gray Herb. 112: 60. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Moquegua (Moquegua).

Voucher. *Weberbauer 7455* (F).

13.50. *Nolana plicata* I. M. Johnst., Contr. Gray Herb. 85: 174. 1929.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Marcona), Dept. Arequipa (Jahuay, Atiquipa).

Voucher. *Dillon et al. 3225* (F).

13.51. *Nolana polymorpha* Gaudich., Voy. Bonite, Bot., pl. 101. 1851.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Lima (Isla San Lorenzo).

Voucher. *Gaudichaud s.n.* (F #1000362).

13.52. *Nolana pterocarpa* Phil., Anales Univ. Chile 91: 27.1895.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Copiapó, Carrizal Bajo).

Voucher. *Dillon & Teillier 5040* (F).

13.53. *Nolana ramosissima* I. M. Johnst., Contr. Gray Herb. 112: 72. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Miguel Díaz, Paposo, La Rinconada, Mantancilla).

Voucher. *Dillon et al. 8085* (F).

13.54. *Nolana rostrata* (Lindl.) Miers ex Dunal, Prodr. 13: 14. 1852.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Bahia Inglesa, Carrizal Bajo) and Prov. Coquimbo (El Tofo).

Voucher. *Dillon & Teillier 5051* (F).

13.55. *Nolana rupicola* Gaudich., Voy. Bonite, Bot., pl. 28.1841.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cerro Moreno, La Chimba, Taltal), Prov. Atacama (Pan de Azúcar, Chañaral, Flamenco, Travesía), and Prov. Coquimbo (Fray Jorge, Coquimbo).

Voucher. *Dillon & Trujillo 8005* (F).

13.56. *Nolana salsoloides* (Lindl.) I. M. Johnst., Contr. Gray Herb. 112: 62. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Paposo, Taltal), Prov. Atacama (Pan de Azúcar, Carrizal Bajo), and Prov. Coquimbo (Ovalle).

Voucher. *Dillon & Trujillo 8047* (F).

13.57. *Nolana scaposa* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 5. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay, Atiquipa, Atico, Camaná).

Voucher. *Dillon et al. 8209* (F).

13.58. *Nolana sedifolia* Poepp., Froriep's Not. Natur-Heilk. 23: 276. 1829.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Tarapacá (Iquique), Prov. Antofagasta (Cobija, Cerro Moreno, La Chimba, Mantancilla, Hueso Parado, Taltal), Prov. Atacama (Caleta Obispito, Travesía), and Prov. Coquimbo (Papudo).

Voucher. *Dillon & Trujillo 8007* (F).

13.59. *Nolana spathulata* Ruiz & Pav., Fl. Peruv. 2: 7, tab. 113a. 1799.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay, Atico, Atiquipa, Mollendo, Cachendo), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande, Tacna).

Voucher. *Dillon et al. 4784* (F).

13.60. *Nolana spergularioides* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 8. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Camaná).

Voucher. *Weigend & Förther 97/766* (F).

13.61. *Nolana sphaerophylla* (Phil.) Mesa, Soc. Biol. Chile, Not. Biol. 6: 199. 1998.

Species distribution. A Chilean species endemic to Prov. Atacama (Quebrada Flamenco, El Salado).

Voucher. *Marticorena 9893* (CONC).

13.62. *Nolana stenophylla* I. M. Johnst., Contr. Gray Herb. 85: 103. 1929.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, La Chimba, Miguel Díaz, Paposo).

Voucher. *Dillon & Dillon 5664* (F).

13.63. *Nolana thinophila* I. M. Johnst., Contr. Gray Herb. 112: 61. 1936.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Marcona), Dept. Arequipa (Jahuay, Lomas, Atico, Ocoña, Camaná, Mollendo, Mejía).

Voucher. *Dillon & Dillon 3851* (F).

13.64. *Nolana tocopillensis* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 78. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cobija, Tocopilla).

Voucher. *Johnston 3603* (GH).

13.65. *Nolana tomentella* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 10. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay).

Voucher. *Dillon et al. 8159* (F).

13.66. *Nolana tovariana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 14. 1955.

Species distribution. A Peruvian species endemic to Dept. Arequipa (Camaná, Ocoña).

Voucher. *Ferreyra 8861* (GH).

13.67. *Nolana villosa* (Phil.) I. M. Johnst., Contr. Gray Herb. 112: 70. 1936.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Cerro Moreno, Punta

Plata, Paposo, San Ramón, Hueso Parado, Taltal, Los Zanjones, Tórtolas) and Prov. Atacama (Caldera), and can range to interior sites above 2000 m.

Voucher. *Dillon et al. 5136* (F).

13.68. *Nolana volcanica* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 12: 3. 1960.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Mollendo).

Voucher. *Dillon et al. 4835* (F).

13.69. *Nolana weissiana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 10: 9. 1955.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Chala, Cháparra, Capac).

Voucher. *Hutchison 1326* (F).

13.70. *Nolana willeana* Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, 12: 1. 1960.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Lomas de Amará).

Voucher. *Kore s.n.* (USM).

14. *Physalis* L.

Solanoideae, Physaleae, Physalinae

Generic distribution. *Physalis* is a Neotropical genus with perhaps 80 species; its highest diversity is in Mexico with ca. 70 species, and a few species are found in the United States, Central America, and the Caribbean. In South America, 12 species are recorded in tropical and subtropical regions; two widespread species are recorded from the *lomas* formations of coastal Peru.

Literature. Macbride (1962), Martínez (1999).

14.1. *Physalis angulata* L., Sp. Pl. 1: 183. 1753.

Species distribution. A species ranging from the United States, Mexico, the Galápagos Islands, and throughout Andean South America to Peru. In Peru, it is widespread in the Andean Cordillera, but only recorded in one *lomas* formation, Dept. La Libertad (Cerro Cabezón).

Voucher. *Leiva et al. 2172* (F).

14.2. *Physalis peruviana* L., Sp. Pl. 2: 1670. 1763.

Species distribution. In Peru, it is widespread in the Andean Cordillera and often cultivated, but only recorded in one *lomas* formation, Dept. Lima (Chorillos).

Voucher. *Gentry & Prance 16455* (F).

15. *Reyesia* Gay

Cestroideae, Salpiglossideae

Generic distribution. *Reyesia* is a Neotropical genus of four species confined to northern Chile, with one reaching adjacent western Argentina.

Literature. Hunziker & Subils (1979b).

15.1. *Reyesia chilensis* Gay, Flora Chilena 4: 418, lam. 52. 1849.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Taltal) and Prov. Atacama (Copiapó, Huasco, Coquimbo).

Voucher. *Dillon & Teillier 5215* (F).

15.2. *Reyesia cactorum* (I. M. Johnst.) D'Arcy, Ann. Missouri Bot. Gard. 65: 712. 1978.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Aguada del Cardon).

Voucher. *Johnston 5258* (GH).

16. *Salpiglossis* Ruiz & Pav.

Cestroideae, Salpiglossideae

Generic distribution. *Salpiglossis* is a Neotropical genus with only two species, both endemic to Chile.

Literature. D'Arcy (1978), Hunziker & Subils (1979b, 1986).

16.1. *Salpiglossis spinescens* Clos, in Gay, Fl. Chilena 5: 127. 1849.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Tierra Amarilla, Chañarcillo).

Voucher. *Werdermann 419* (F).

17. *Schizanthus* Ruiz & Pav.

Schizanthoideae, Schizantheae

Generic distribution. *Schizanthus* is a Neotropical genus of 9 to 12 annual species largely confined to Chile; two species are disjunct to adjacent Argentina.

Literature. Grau & Gronbach (1984), Hunziker (1979, 2000).

17.1. *Schizanthus candidus* Lindl., Bot. Reg. 29, t. 45. 1843.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Carrizal Bajo).

Voucher. *Philippi s.n.* (SGO #55393).

17.2. *Schizanthus integrifolius* Phil., Anales Univ. Chile 43: 530. 1873.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Atacama (Chañaral) and Prov. Coquimbo (Vicuña), and occurring in both high and low elevations.

Voucher. *Marticorena et al. 1586* (F).

17.3. *Schizanthus lacteus* Phil., Reise Atacama 46. 1860.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Paposo, Taltal).

Voucher. *Dillon et al. 5744* (F).

17.4. *Schizanthus laetus* Phil., Reise Atacama 45. 1860.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (Tocopilla, Paposo, Taltal).

Voucher. *Dillon & Teillier 5173* (F).

18. *Solanum* L.

Solanoideae, Solaneae

Generic distribution. *Solanum* is a cosmopolitan genus of ca. 1250 species, with estimates of 850 species from South America. Within the *lomas* formations of Chile and Peru, 21 species are represented, and among these, five have traditionally been treated under *Lycopersicon*.

Literature. Correll (1967), D'Arcy (1972), Edmonds (1972), Hawkes (1990), Johnston (1931), Macbride (1962), Nee (1999), Ochoa (1962), Olmstead & Palmer (1997), Rick (1986), Rick & Lamm (1955), Rick & Tanksley (1981), Rick et al. (1977, 1979), Ugent (1975).

18.1. *Solanum brachyantherum* Phil., Anales Univ. Chile 43: 522. 1873.

Species distribution. A Chilean species endemic to *lomas* formations of Prov. Tarapacá (Iquique) and Prov. Antofagasta (Tocopilla, La Chimba, El Cobre, Miguel Díaz, Paposo, Taltal).

Voucher. *Dillon et al. 5534* (F).

18.2. *Solanum chancayense* Ochoa, Agronomía (Lima) 26: 316. 1959.

Species distribution. A Peruvian species endemic to *lomas* formations of Dept. La Libertad (Cerro Cabras, Cerro Chipitur) and Dept. Lima (Lachay, Chancay, Quilmaná).

Voucher. *Ochoa 11765* (F).

18.3. *Solanum chilense* (Dunal) Reiche, Fl. Chile 5: 358. 1910.

Species distribution. A species widely distributed in coastal localities from southern Peru to northern Chile. Within the *lomas* formations of Peru, it ranges from Dept. Moquegua and Dept. Tacna, south to Prov. Tarapacá (Azapa, Iquique) and in Chile, Prov. Antofagasta (Tocopilla, Paposo, Taltal). In floras recognizing *Lycopersicon*, this species is treated as *L. chilense* Dunal, *L. atacamensis* Phil., or *L. bipinnatifidum* Phil.

Voucher. *Dillon et al. 5560* (F).

18.4. *Solanum ferreyrae* Ugent, Phytologia 31: 18. 1975.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Arequipa (Jahuay).

Voucher. *Ferreyra 1523* (USM).

18.5. *Solanum fragile* Wedd., Chlor. Andina 2: 105. 1859.

Species distribution. A species widely distributed throughout the Andean Cordillera from Ecuador, Peru, Chile, and Argentina. The type was collected in southern Peru (Dept. Tacna) at elevations > 3000 m. Though collections from the *lomas* formations have been annotated as *S. fragile*, the species encountered from Dept. Arequipa (Atiquipa) appear distinct and possibly represent an undescribed species.

Vouchers. *Ochoa & Salas 14901* (F), *Weigend & Förther 97/925* (F), *Worth & Morrison 15704* (F).

18.6. *Solanum habrochaites* S. Knapp & D. M. Spooner, Novon 9: 375. 1999.

Species distribution. A widespread species from southwestern Ecuador to south-central Peru. Within the *lomas* formations, it is restricted to Dept. La Libertad (Cerro Campana, Cerro Cabezón, Cerro Cabras). This species has been treated as *Solanum agrimoniifolium* Dunal, or in treatments recognizing *Lycopersicon* as *L. hirsutum* Dunal.

Voucher. *Dillon et al. 4665* (F).

18.7. *Solanum immite* Dunal, Prodr. 13: 32. 1852.

Species distribution. A widespread Peruvian species from the Andean Cordillera and coastal habitats. In the *lomas* formations, it is recorded from Dept. La Libertad (Virú) and Dept. Lima (Supe, Chancay).

Voucher. *Bernardi 16413* (F).

18.8. *Solanum medians* Bitter, Repert. Spec. Nov. Regni Veg. 11: 366. 1912.

Species distribution. A widespread Peruvian species from the Andean Cordillera and coastal habitats. In the *lomas* formations, it is recorded from Dept. Lima (Quilmaná, Cerro Agustino), Dept. Arequipa (San Juan, Camaná, Atiquipa, Chala), Dept. Moquegua (Ilo), and Dept. Tacna (Sama Grande).

Voucher. *Ochoa & Salas 14900* (F).

18.9. *Solanum mochiquense* Ochoa, Agronomía (Lima) 26: 111. 1959.

Species distribution. A widespread Peruvian species from the eastern lowlands to coastal habitats. In the *lomas* formations, it is known from Dept. La Libertad (Cerro Campana, Cerro Chipitur, Cerro Cabras, Virú).

Voucher. *Angulo 1213* (F).

18.10. *Solanum montanum* L., Sp. Pl. 1: 186. 1753.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Lambayeque (Cerro Reque), Dept. La Libertad (Cerro Chipitur, Cerro Campana, Cerro Cabras, Virú), Dept. Ancash (Casma), Dept. Lima (Lachay, Pasamayo, Chorrillos, Amancaes, Atocongo, Manzano, Lupín, Pachacamac), and Dept. Arequipa (Capac, Atiquipa). The synonym *S. tuberiferum* Dunal has been applied to this species.

Voucher. *Dillon et al. 4685* (F).

18.11. *Solanum multifidum* Lam., Tabl. Encycl. 2: 17. 1794.

Species distribution. A widespread Peruvian species from the Andean Cordillera to coastal habitats. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Cabras), Dept. Ancash (Lupín), Dept. Lima (Pasamayo), Dept. Arequipa (Caravelí, Atico, Mollendo, Cachendo), and Dept. Tacna (Tacna). The synonym *S. senecioides* Dunal has been applied to this species.

Voucher. *Dillon et al. 4741* (F).

18.12 *Solanum murphyii* I. M. Johnst., Contr. Gray Herb. 95: 34. 1931.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Ica (Isla San Gallán, Islas de las Viejas).

Voucher. *Murphy 3219* (GH).

18.13. *Solanum neoweberbaueri* Wittm., Bot. Jahrb. Syst. 50 (Suppl.): 540. 1914.

Species distribution. A Peruvian species ranging from high-elevation localities in the central Andean Cordillera and recorded from the *lomas* formations of Dept. Lima (Morro Solar, Chorrillos).

Voucher. *Weberbauer 5683* (F).

18.14. *Solanum pennelii* Correll, Madroño 14: 233. 1958.

Species distribution. A widespread Peruvian species from the Andean Cordillera and recorded from the *lomas* formations of Dept. La Libertad (Cerro Cabezón, Virú), Dept. Ica (Nasca), and Dept. Arequipa (Chala). In floras recognizing *Lycopersicon*, this species has been treated as *Lycopersicon pennellii* (Correll) D'Arcy.

Voucher. *Leiva et al. 2193* (F).

18.15. *Solanum peruvianum* L., Sp. Pl. 186. 1753.

Species distribution. A species recorded from the Andean Cordillera and coastal habitats. It is widespread in the *lomas* formations, occurring in Peru from Dept. La Libertad (Cerro Cabezón, Cerro Campana, Cerro Prieto, Cerro Chiputur, Virú), Dept. Lima (Lachay, Iguanil, Amancaes, Cerro Agustino, Atocongo), Dept. Arequipa (Atiquipa, Capac, Atico, Camaná, Mollendo), and Dept. Tacna (Pampa Mogollo), and in northern Chile, Prov. Tarapacá (Azapa). In floras recognizing *Lycopersicon*, this species has been treated as *L. hirsutum* Dunal or *L. peruvianum* (L.) Mill.

Voucher. *Dillon et al. 4665* (F).

18.16. *Solanum phyllanthum* Cav., Ic. 4: 35, tab. 359, fig. 2. 1797.

Species distribution. A widespread species recorded from the *lomas* formations of northern Chile, Prov. Antofagasta (Paposo) and Peru from Dept. La Libertad (Cerro Campana) and Dept. Lima (Chancay, Amancaes). The synonym *S. paposanum* Phil. has been applied to this species.

Voucher. *Dillon et al. 2720* (F).

18.17. *Solanum pimpinellifolium* L., Cent. Pl. 1: 8. 1755.

Species distribution. A widespread species ranging from the Andean Cordillera of southern Ecuador to Peru. In the *lomas* formations, it is recorded from Dept. La Libertad (Cerro Campana), Dept. Lima (Atocongo, Amancaes, Pachacamac), and Dept. Tacna (Sama Grande). In treatments recognizing *Lycopersicon*, this species has been treated as *L. pimpinellifolium* (L.) Mill.

Voucher. *Dillon et al. 2703* (F).

18.18. *Solanum radicans* L.f., Dec. Pl. Horti Upsal. 1, tab. 10. 1762.

Species distribution. A Peruvian species widespread from the eastern lowlands, Andean Cordillera, and coastal habitats. In the *lomas* formations it is recorded from Dept. La Libertad (Cerro Campana), Dept. Arequipa (Mollendo), Dept. Moquegua (Ilo), and Dept. Tacna (Pampa Mogollo).

Voucher. *Dillon et al. 4755* (F).

18.19. *Solanum remyanum* Phil., Anales Univ. Chil. 91: 17. 1895.

Species distribution. A Chilean species endemic to the *lomas* formations of Prov. Antofagasta (El Cobre, Paposo, Taltal), Prov. Atacama (Pan de Azúcar, Pampa de Caracoles), and Prov. Coquimbo (Punta Arrayán).

Voucher. *Dillon et al. 5477* (F).

18.20. *Solanum tuberosum* L., Sp. Pl. 1: 185. 1753.

Species distribution. A widespread species in the Andean Cordillera as a cultivated herb and the source of potatoes. It is a rare in Peruvian *lomas* formations, but has been encountered as a cultivated species during El Niño events when local inhabitants take advantage of increased soil moisture to cultivate various crops.

Voucher. No voucher seen, but the author has observed it cultivated in Dept. La Libertad (Cerro Cabezón).

18.21. *Solanum wittmackii* Bitter, Repert. Spec. Nov. Regni Veg. 12: 54. 1913.

Species distribution. A Peruvian species endemic to the *lomas* formations of Dept. Lima (Amancaes, San Gerónimo).

Voucher. *Macbride 5890* (F).

8

THE SOLANACEAE IN THE FLORA OF TROPICAL EAST AFRICA

Jennifer M. Edmonds

Abstract. The taxonomic treatment of the Solanaceae for the *Flora of Tropical East Africa* recently began at the Royal Botanic Gardens, Kew, where the overall project is based. An overview of the taxa collected from Kenya, Tanzania, and Uganda deposited in the herbaria of the RBG, Kew, and The Natural History Museum, London, has indicated that over 100 species belonging to 21 genera are found in this region. However, only 4 of these genera include species that are endemic to the area, with the remaining 17 being represented by species introduced either deliberately or accidentally. Using the infrafamilial classification proposed by D'Arcy, the relevant genera are reviewed. Most are represented by only one to a few species, apart from *Solanum* L., which exhibits its usual taxonomic complexity and diversity, and has over 70 species occurring in these countries. The species so far recognized are briefly considered, particularly with regard to their origin, distribution, and economic importance in this area.

Key words: *Browallia*, *Brugmansia*, *Brunfelsia*, *Capsicum*, *Cestrum*, *Cyphomandra*, *Datura*, *Discopodium*, *Iochroma*, Kenya, *Lycium*, *Lycopersicon*, *Nicandra*, *Nicotiana*, *Petunia*, *Physalis*, *Schizanthus*, *Schwenckia*, Solanaceae, *Solandra*, *Solanum*, *Streptosolen*, Tanzania, Tropical East Africa, Uganda, *Withania*.

The *Flora of Tropical East Africa* (FTEA) is a project based at the Royal Botanic Gardens, Kew, which officially began in 1949, although work had already started on it before the advent of the Second World War. The *Flora* was to treat all 12,000 species of wild plants occurring in Kenya, Tanzania, and Uganda, thus covering a total surface area of 1,768,047 square kilometers, extending from latitude 4°30'N to 11°40'S and longitude 29°30'E to 42'E, and from sea level to 5870 m (Turrill & Milne-Redhead, 1952). To date, systematic accounts have been completed and published for some 8000 of these species, representing approximately 66% of the total. Accounts for the remaining 4000 species will be completed by 2005. The *Flora* is published in separate parts, with each part treating a family. In many groups or families of plants, no such treatments have appeared before, and in such cases this *Flora* is not only the first to treat the group, but also the first to give a biodiversity listing and to provide an identification key. The published treatments include full descriptions, synonymy, notes on habitat and distribution both within and outside the FTEA area, and illustrations, as well as the identification keys. The treatments therefore comprise a series of regional monographs. The notable editors of this flora include Edgar Milne-Redhead (with W. B. Turrill from 1952 to 1958, with C. E. Hubbard from 1958 to 1966, and with R. M. Polhill from 1966 to 1972) and Roger Polhill (from 1973 to 1997); the current editor is Henk Beentje (1998–).

Of the 4000 species still to be treated, those belonging to the Solanaceae probably constitute one of the biggest problems. The family has never been revised in the East African region, and the African species belonging to the genus *Solanum* are considered to be particularly complex taxonomically. With this in mind, together with the impending deadline of 2005 for the completion of the entire *Flora of Tropical East Africa*, I agreed to undertake the revision of the family in this floral region. The work formally began in October 2000, was unavoidably halted for six months in 2001, and is now scheduled to be completed late in 2005. This paper represents a taxonomic summary of the family as perceived at the start of this project.

An overview of the genera and species represented in Kenya, Tanzania, and Uganda, based on specimens in K, and augmented by those at BM, has indicated that the representatives of this family number over 100 species and belong to 21 genera. The present account adopts the infrafamilial classification proposed and subsequently revised by D'Arcy (1975, 1979, 1991), who did so much to stimulate interest in the classification and phylogeny of this family. His papers on the subject displayed not only the depth of his knowledge and perception on the many subjects now integral to systematics, but also his ability to utilize and integrate historical, morphological, phytogeographical, macromolecular, and cladistic studies to elucidate relationships within the Solanaceae and also those between it and other families. In his last published overview of the family, D'Arcy (1991) estimated that the Solanaceae were composed of 96 genera with approximately 2300 species, though he considered this conspectus to be only temporary, with information lacking for many parts. During the past decade, modified classificatory schemes of the Solanaceae have indeed been proposed, some of the most recent being those of Olmstead et al. (1999) based on chloroplast DNA sequence data and by Hunziker (2001) based on morphological, karyological, and phytochemical data combined with information available from the vast amount of literature published on this family. The interrelationships of the solanaceous genera will undoubtedly continue to be reviewed and adjusted in the light of new data providing further insight into their phylogeny.

Following D'Arcy (1991), the genera represented in tropical East Africa belong to the two subfamilies Cestroideae and Solanoideae. Those from the Cestroideae belong to four tribes and include *Cestrum* L. from the Cestreae, *Nicotiana* L. and *Petunia* Juss. from the Nicotianeae, *Browallia* L., *Brunfelsia* L., *Schizanthus* Ruiz & Pav., and *Streptosolen* Miers from the Salpiglossideae, and *Schwenckia* L. from the Schwenckieae. The Solanoideae are represented by six tribes and include the genera *Brugmansia* Pers. and *Datura* L. from the Datureae, *Discopodium* Hochst. from the Jaboroseae, *Lycium* L. from the Lycieae, *Nicandra* Adans. from the Nicandreae, *Solandra* Sw. from the Solandreae, and *Capsicum* L., *Cyphomandra* Mart. ex Sendtn., *Iochroma* Benth., *Lycopersicon* Mill., *Physalis* L., *Solanum* L., and *Withania* Pauquy from the Solaneae. This infrafamilial classification broadly agrees with the latest revision by Hunziker (2001) apart from his inclusion of *Discopodium* in the tribe Solaneae, and in his treatment of the Salpiglossideae. Of the genera included in this tribe by D'Arcy, Hunziker treated *Schizanthus* as the monotypic subfamily Schizanthoideae, while *Browallia* and *Streptosolen* are placed in the tribe Browallieae, and *Streptosolen* in the tribe Francisceae of the subfamily Cestroideae.

Compared with the rest of the world, and particularly with Central and South America where the family shows its greatest diversity, African Solanaceae are neither numerous nor distinct (D'Arcy, 1991), with D'Arcy only considering *Discopodium* and *Withania* to be truly African genera. Most of the genera are represented by one to a few species in this area, where they include many introduced and economically important species as well as those of considerable medicinal and poisonous value and a number of widely planted ornamentals. In many cases the genera are only represented by introduced species. The exception is the genus *Solanum*, which in line with its reputation and behavior elsewhere, constitutes the largest and most taxonomically complex genus, and has over 70 species occurring in this region.

The specific names used throughout are those taken from the Kew specimens. No taxonomic revision has yet been attempted on these taxa; some of the specific epithets used are undoubtedly wrong or synonyms of other taxa, and many will inevitably change during the treatment of this family for the FTEA. Résumés of the generic limits and distributions have been taken from many papers and floristic accounts. These have proved to be extremely variable from author to author (e.g., D'Arcy, 1979, 1991; Hepper, 1998; Hunziker, 1979, 2001; Schultes & Raffauf, 1991), again emphasizing the taxonomic complexity of this family. The suprageneric authorities have been taken from the *Index Nominum Supragenericorum Plantarum Vascularium* website compiled by James L. Reveal. These often differ from those cited by other authors, particularly by Hunziker (2001). The generic authorities and type species have been taken and verified from the *Index Nominum Genericorum* by Farr et al. (1979a, 1979b, 1979c) and from *Names in Current Use for Extant Plant Genera* by Greuter et al. (1993). In the case of Linnean genera, the type specimen citation has been taken from Jarvis et al. (1993), where details of their publication may also be found. Where possible, the illustrations used have been selected from older literature. These, in addition to their aesthetic clarity, often portray both flowering and fruiting aspects of the plants.

GENERA FOUND IN TROPICAL EAST AFRICA

CESTROIDEAE Burnett

Cestreae Dumort.

Cestrum L., Sp. Pl. 191. 1753; Gen. Pl. ed. 5, 88. 1754. TYPE SPECIES: *Cestrum nocturnum* L. Figure 1.

This is the second largest genus in the family, with over 250 described species, though Nee (2001) recently proposed that the correct number is closer to 150. The species are woody shrubs and small trees, which are often found in warm parts of Mexico, Central America, the Antilles, and in the Andes of South America, but which are now naturalized and widely cultivated as ornamentals in many parts of the world. Among the generic characters illustrated in Figure 1 are the entire leaves, the campanulate calyx, the tubular corolla constricted at the throat with five spreading lobes and with the filaments adnate mid-way with included anthers, the filiform style, and the baccate fruit. In addition, this figure shows the narrowly lanceolate leaves and the flowers borne in terminal or lateral panicles, which are characteristic of *Cestrum parqui* L'Hér.

Eight *Cestrum* species have been recorded from the "wild" or in cultivation in the FTEA region. *Cestrum nocturnum* L. occurs in all three countries; *C. aurantiacum* Lindl., *C. elegans* (Brongn. ex Neumann) Schltdl., *C. fasciculatum* (Schltdl.) Miers, and *C. parqui* L'Hérit. have been collected from Kenya and Tanzania; *C. diurnum* L. and *C. thyrsoideum* HBK from Kenya and *C. cultum* Francey from Tanzania.

Nicotianeae Dumort.

Nicotiana L., Sp. Pl. 180. 1753; Gen. Pl. ed. 5, 84. 1754. TYPE SPECIES: *Nicotiana tabacum* L. Figure 2.

Nicotiana is composed of 60 to 95 mainly herbaceous species that are found in subtropical parts of the Americas, the Pacific, Australia, and Africa (Namibia, where *N. africana* Merxm. is considered to be native). Five species have been recorded from the FTEA region, where they are mostly naturalized. The most infamous of these is *N. tabacum* L., popularly known as tobacco. This species, which is the generic type species, is native to the New World, probably originating in northwest Argentina (Hunziker, 2001), but it is now extensively grown throughout the world for smoking, chewing, and snuff manufacture, with the toxic alkaloid nicotine also being used as a powerful insecticide. Many varieties and cultivars of this species are widely grown as fragrant ornamentals. *Nicotiana tabacum* now occurs throughout Kenya, Tanzania, and Zanzibar, where it is also widely cultivated for its stimulatory effect, with many varieties being grown as fragrant ornamentals. A further four *Nicotiana* species have been recorded from the East African region. Both *N. alata* Link & Otto and *N. suaveolens* Lehm. are found in Tanzania, *N. glauca* R. C. Graham in Kenya, and *N. rustica* L. in all three FTEA countries. Some of these species are also cultivated as ornamentals, e.g., *N. alata* var. *grandiflora* in Tanzania.

Generic characters illustrated in Figure 2 include the terminal paniculate inflorescences, the tubular-campanulate calyces, the long tubular-infundibuliform corollas, and the capsulate fruit with minute seeds. Among the characters typical of *Nicotiana tabacum* visible in this figure are the large ovate-lanceolate leaves with acute apices, the conspicuous pubescence covering all parts of the plant, and the erect flowers.

Petunia Juss., Ann. Mus. Nat. Hist. Par. 2, 215, t. 47. 1803, nom. conserv. TYPE SPECIES: *Petunia nyctaginiflora* Juss. (typ. conserv.). Figure 3.

Petunia is now considered to be composed of only 3 herbaceous species, though some authors recognize as many as 40 species (Hunziker, 1979). Recently, Hunziker (2001) proposed that *Petunia* is an American genus, with 33 species occurring in central and southern South America, but with an additional species (*P. parviflora* Juss.) showing a disjunct distribution and also occurring in the Northern Hemisphere in the United States, Cuba, and Mexico. It is another solanaceous genus widely cultivated throughout the world for its ornamental beauty. *Petunia hybrida* Hort. ex Vilm. is grown in the Cultivated Flora of the City Park, Nairobi, Kenya; it is often known as the "Common Garden Petunia" and undoubtedly occurs as an escape elsewhere in the FTEA region.

The large solitary flowers that characterize this genus are clearly apparent in Figure 3, as are the infundibuliform corollas, the deeply 5-lobed calyces with the lobes somewhat linear and spreading, the subequal adnate stamens, and again the conspicuous pubescence throughout.

Salpiglossideae Benth.

Browallia L., Sp. Pl., 631. 1753; Gen. Pl. ed. 5, 278. 1754. TYPE SPECIES: *Browallia americana* L. Figure 4.

This is generally considered to be a small Neotropical genus of two (D'Arcy, 1979; Hunziker, 1979), three (D'Arcy, 1991), or six (Hunziker, 2001) herbaceous annual species, extending from southern Mexico through Central America to Bolivia (Hunziker, 1979). However, Schultes and Raffauf (1991) mentioned 25 species occurring in tropical America and the West Indies, while Hunziker (2001) recently suggested that the generic range extends from southern Arizona to andine South America. The species are often grown as ornamental bedding or pot-plants and are widely naturalized. *Browallia* plants identified as *B. viscosa* HBK are cultivated in both Kenya and Uganda, and also occur as a weed of cultivation in Tanzania. However, this species is thought to be synonymous with the extremely variable *B. americana.*

The relatively few-flowered inflorescences borne in upper leaf axils characteristic of this genus are clearly shown in Figure 4, as are the tubulate-campanulate toothed calyces and the zygomorphic tubular hypercrateriform corollas with five bilabiate lobes.

Brunfelsia L., Sp. Pl. 191. 1753 ("*Brunsfelsia*"); Gen. Pl. ed. 5, 87. 1754 (nom. et orth. conserv.). TYPE SPECIES: *Brunfelsia americana* L. Figure 5.

Brunfelsia is a woody tropical genus from South and Central America of 40 to 45 species of shrubs and small trees, many of which are cultivated for their ornamental and medicinal value (cf. Hunziker, 1979). Plowman (1979) considered that the genus originated in northern South America from where it differentiated into three distinct lines of evolution, one in the Caribbean region (where he considered 21 species to be endemic to the West Indies), one in the Amazonian lowlands, and the third adapted to upland forest hillsides in the Andes and southeastern Brazil. *Brunfelsia americana* L., which is sometimes known as Lady of the Night, *B. uniflora* (Pohl) D. Don and *B. hopeana* Benth. (thought to be synonymous with *B. uniflora*), have all been recorded in Tanzania, and *B. uniflora* is also cultivated in Kenya.

Generic characters illustrated in Figure 5 include the tubular-campanulate five-dentate calyces; the much longer cylindrical corolla tube with five somewhat recurved broad lobes; the four included fertile stamens, with the upper pair (lateral) having longer filaments than the lower (posterior) pair and all four attached to the upper part of the hypercrateriform corolla; the long filiform curved style with the prominently bilobed stigma, and the conical ovary with many ovules. In *B. hopeana* (? = *B. uniflora)*, the species illustrated, the cymes are reduced to single flowers.

Schizanthus Ruiz & Pav., Fl. Peruv. Prodr. 1, 6. 1794; Fl. Peruv., 1, 13, tab. 17. 1798. TYPE SPECIES: *Schizanthus pinnatus* Ruiz & Pav. Figure 6.

Schizanthus is composed of 8 to 20 species of annual herbs that are all native to Chile. *Schizanthus pinnatus* Ruiz & Pav., the type species, is widely cultivated as a colorful ornamental throughout the world. It is often known as the Poor Man's Orchid or Butterfly-flower and is recorded as naturalized in Tanzania. Generic characters illustrated in Figure 6 include the cymose inflorescences, the five-partite calyx, the irregular flowers with bilabiate corollas in which the upper and lower lips are three-lobed, and the small capsulate fruits. The specific epithet of the type species describes the distinctly pinnatisect leaves.

Streptosolen Miers, Ann. & Mag. Nat. Hist. Ser. II, 5, 208. 1850. TYPE SPECIES: *Streptosolen jamesonii* (Benth.) Miers ("*jamesoni*") (*Browallia jamesonii* Benth. ("*jamesoni*"). Figure 7.

This is a monospecific suffruticose genus found at higher elevations in Peru, Ecuador, and possibly also southern Colombia, which is often grown as an ornamental for its colorful orange flowers. *Streptosolen jamesonii* (Benth.) Miers is cultivated in both Kenya and Tanzania. Characteristic generic features illustrated in Figure 7 include the conspicuous pubescence covering all vegetative and floral parts, the ovate leaves, and the flowers in subcorymbose cymose inflorescences with tubular toothed calyces and infundibuliform five-lobed corollas.

Schwenckieae A. T. Hunz.

Schwenckia L., Gen. Pl. ed. 6, ("567") 577. 1764 (*"Schwenkia")*. TYPE SPECIES: *Schwenckia americana* L. Figure 8.

Schwenckia is a New World genus of 5 to 30 largely herbaceous species occurring from the Antilles and Central America through northern and eastern South America to Argentina, and showing its greatest diversity in Brazil. *Schwenckia americana* L. is now a widespread weed throughout tropical Africa and occurs in both Tanzania and Uganda. Symon (1991) considered it to be an adventive in Africa that had arrived through involuntary transport by man, a view endorsed by D'Arcy and Benítez de Rojas (1991).

Most of the delimiting generic characters are clearly illustrated in Figure 8. These include the sparse pubescence covering the entire plant; the upper sessile narrowly oblong leaves; the lax paniculate inflorescence; the cylindrically tubular calyces with five calyx teeth; the narrowly tubular corollas in which the small obtusely triangular apical lobes alternate with clavate processes; the two fertile stamens with ellipsoidal anthers; the long filiform smooth style; the bilocular ovary; the subglobose capsulate bivalvate fruit surrounded by the persistent calyx; and the small seeds with reticulate testas.

SOLANOIDEAE Kostel

Datureae Dumort.

Brugmansia Pers., Syn. Pl., 1, 216. 1805. TYPE SPECIES: *Brugmansia ×candida* Pers. (*Datura arborea* Ruiz & Pav. *non* L.). Figure 9.

Brugmansia is a genus of 5 to 15 arborescent species with large pendulous flowers that are native to South America but which have been widely planted as ornamentals and hedging plants in the tropics and subtropics of many parts of the world. Some of the species are considered to be natural hybrids, and there are many races and cultivars. They have often been included as a section of the genus *Datura* L., following Linnaeus's treatment in 1753 (cf. Lockwood, 1973). Nee (1991), while conceding that the daturas and brugmansias represent two distinct groups, suggested their recognition as subgenera of *Datura*. However, most authors now consider them to be distinct genera. Lockwood (1973), for example, clearly presented anatomical, morphological, and ecological evidence for the generic recognition of *Brugmansia*, while Persson et al. (1999) convincingly reinforced this conclusion using pollen morphology and phylogenetic analyses.

Brugmansia plants are often known as tree daturas, floripondios, or Angel's Trumpet, and three species have been recorded from the FTEA region: *B. suaveolens* (Humb. & Bonpl. ex Willd.) Bercht. & Presl from all three countries; *B. ×candida* Pers. from Kenya and Tanzania, and a taxon identified as *B. arborea* (L.) Lagerh. from Tanzania, which is thought to be synonymous with *B. ×candida*. The aborescent habit of this genus is illustrated in Figure 9, together with the large, glabrous repand leaves, the solitary, pendulous large flowers with a zygomorphous calyx, the broadly infundibuliform corolla with five recurved large petals, and the long-exserted styles with small elongate stigmas. The spathate calyx characteristic of the species *B. ×candida* (with which *B. arborea* Ruiz & Pav. is synonymous) is also clearly evident.

Datura L., Sp. Pl. 179. 1753; Gen. Pl. ed. 5, 83. 1754. TYPE SPECIES: *Datura stramonium* L. Figure 10.

Datura is a New World genus collectively known as the Thorn Apples, which is composed of 7 to 12 species of annual or semi-perennial herbs and shrubs with erect flowers. *Datura* is now recognized as having a relatively restricted natural distribution, being native to semiarid parts of Mexico and the southwestern U.S. (cf. Hunziker, 2001). All Old World daturas were introduced from the Americas, mostly by Portuguese traders, during the early years of the intensive European colonization of the New World (cf. Symon & Haegi, 1991; Persson et al., 1999). Three naturalized species—*D. innoxia* Mill., *D. metel* L., and *D. stramonium* L.—are found throughout the East African region, where they are probably widely cultivated for their hallucinogenic and medicinal effects as well as for their ornamental value and their narcotic properties.

The many generic characters illustrated in Figure 10 include the ovate alternate leaves; the solitary erect flowers with the elongated tubular five-lobed calyces, which are basally circumsessile and the large, infundibuliform corollas with the long slender tube and cuspidate lobes; the five stamens alternating with the corolla lobes with long slender glabrous filaments and ellipsoidal basifixed anthers; the glabrous filiform style with a bilobed stigma; the conical superior ovary, which is 2-loculate above but 4-loculate basally owing to a false septum; the capsulate valvate fruits subtended by the cupular remains of the calyx; and the discoid seeds. Figure 10 also shows many features distinguishing the type species *D. stramonium*. These include the smooth, stout, glabrous stems; the ovate sinuate-dentate leaves; the shortly cuspidate corollas; the included filaments and style; and the conspicuously spiny 4-valvate capsules, which are always erect.

Jaboroseae Miers

Discopodium Hochst., Flora 27, 22. 1844.
TYPE SPECIES: *Discopodium penninervium* Hochst. Figure 11.

Discopodium is considered to be a monospecific genus restricted to higher altitudes of isolated mountain forests of east, west, and central tropical Africa, and the shrubby *D. penninervium* Hochst. is found throughout the FTEA region. The species *D. eremanthum* Chiov., described as a shrub or tree with fewer-flowered fascicles in Kenya and Uganda (cf. Beentje, 1994), may prove to be either a distinct species or only a variant of *D. penninervium.*[1] Populational differences in this species were also recognized by Bitter (cf. Symon, 1991), indicating that the infrageneric morphological variation exhibited in this region clearly requires further investigation.

Among the features characteristic of the genus illustrated in Figure 11 are the prominently penninervate leaves, and the few- to many-flowered axillary fasciculate epedunculate inflorescences with five-merous flowers borne on slender pedicels. The floral dissections of this figure also clearly show the distinct broadly campanulate calyx with broadly triangular sepals; the urceolate corolla with narrowly triangular reflexed petals; the included adnate equal stamens with filiform filaments and bithecate anthers; the annular disc subtending the conical ovary with axile placentation; and the baccate fruit with sub-reniform vesciculate seeds.

Although D'Arcy (1991) placed *Discopodium* in the tribe Jaboroseae, Olmstead et al. (1999) later included this genus in the tribe Solaneae in their provisional classification of the family largely based on chloroplast DNA studies. In his recent book, Hunziker (2001) similarly included *Discopodium* in the tribe Solaneae, but in the subtribe Witheringinae together with eight other genera largely on the basis of their common lack of filament enlargement, considering D'Arcy's (1991) inclusion of it in the Jaboroseae to be "an irrelevant decision." The genus *Discopodium* shows affinity with *Withania*, and Symon (1991) suggested that these two genera together with a third — *Mellissia* Hook., a critically endangered endemic found on St. Helena—represent a phytogeographically coherent suite of a distinctive African element of the Solanaceae. He further proposed that these three genera constitute a Gondwanan element.

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[1] Recent morphological and field work has demonstrated that this genus is indeed composed of two distinct species, with the rarer *D. eremanthum* being restricted to higher altitudes of isolated mountain forests (cf. Edmonds, J.M. The genus *Discopodium* Hochst. (Solanaceae) in Africa. Proc. XVIIth. AETFAT Congress, Addis Ababa, 2003 (in press)).

Lycieae Lowe

Lycium L., Sp. Pl. 191. 1753; Gen. Pl. ed. 5, 88. 1754. TYPE SPECIES: *Lycium afrum* L. Figure 12.

Lycium is a large genus of 75 to 100 species of shrubs or small trees, which are found throughout the world; they are often referred to as Box-thorns or Matrimony-vines. According to Symon (1991) there are three main areas of diversity—South Africa, North America, and South America, with differentiation of the African and South American suites being maintained at a sectional level. Although the majority of species are found in temperate and subtropical regions of the Americas, around 30 to 40 species are probably native to the Old World (cf. Hunziker, 1979, 2001). Both *L. europaeum* L. and *L. shawii* Roem. & Schult. have been recorded from all three FTEA countries, but Venter (pers. comm.) considers many specimens to have been misidentified and believes that only *L. shawii* occurs throughout this region.

Among the generic features visible in Figure 12 are the woody stems with caulinar spines, the simple entire leaves, the flowers with short campanulate/tubular calyces, and infundibuliform corollas with five reflexed broad lobes. This figure also shows the flowers arising singly or in pairs from clusters of leaves, and exserted anthers and styles.

Nicandreae Lowe

Nicandra Adans., Fam. Pl. 2, 219. 1763, nom. cons. TYPE SPECIES: *Nicandra physalodes* (L.) Gaertn. (*"physaloides"*) (*Atropa physalodes* L.), (typ. conserv.). Figure 13.

Nicandra is another monospecific genus, with *N. physalodes* (L.) Gaertn. generally being regarded as native to Peru and possibly northern Argentina (cf. Hunziker, 2001). This species is often called Apple-of-Peru, and it now occurs as a widespread casual herb throughout warmer parts of the world, where it is also cultivated as an ornamental. It has been collected from both Kenya and Tanzania, and is cultivated in parts of Tanzania.

Figure 13 elegantly illustrates the many features characterizing *Nicandra physalodes.* These include the large, broadly ovate, sinuate leaves and the solitary showy flowers, which are erect at first but become nodding. The distinctive calyx has five broadly ovate, acute, prominently veined, accrescent lobes, which are cordate at the base; these enclose the lower half of the corolla and later the entire fruit. The corolla is broadly campanulate with five shallow, quincuncial, bilobed, reflexed petals. The five stamens are included with short filaments and bilobed anthers; the style is also included with a capitate stigma, and the ovary is conical. The baccate fruit is completely enclosed by the accrescent chartaceous calyx, and the numerous seeds are discoidal.

Solandreae Miers

Solandra Sw., Kongl. Vet. Akad. Nya. Handl. Stock. 8, 300, t. 11. 1787, nom. conserv. TYPE SPECIES: *Solandra grandiflora* Sw. Figure 14.

Solandra is a Neotropical genus of eight to ten species of woody climbers that occur from Mexico and the West Indies to Peru, Bolivia, and southeastern Brazil, and which are often known as Chalice-vines. *Solandra grandiflora* Sw. is an ornamental climber, widely cultivated for its spectacular flowers, especially in Nairobi, Kenya, where hybrid forms between this species and *S. hartwegii* N. E. Brown (= *S. maxima* (Sessé & Moc.) P. S. Green) have been produced as ornamentals in the City Park.

Generic features shown in Figure 14 include the large, conspicuous flowers, which as here are often borne singly and on stout woody pedicels. The calyx is tubular and slightly zygomorphic; the corolla greatly exceeds the calyx, is somewhat cyathiform with a long basal tube and prominent venation, and the five petal lobes are recurved, often with laciniate margins; the five stamens are subequal and the style slender and declinate with a small globular stigma.

Solaneae Dumort.

Capsicum L., Sp. Pl. 188. 1753; Gen. Pl. ed. 5, 86. 1754. TYPE SPECIES: *Capsicum annuum* L. Figure 15.

Capsicum is an economically important genus of herbs or slender shrubs, whose 10 to 50 species are native to Central and South America, though some species constitute major spice and vegetable crops throughout the world. The species are universally known as peppers, and cayenne, chili, sweet, green and red peppers are widely cultivated and naturalized throughout Africa. The three common domesticated species, *C. annuum* L., *C. baccatum* L., and *C. frutescens* L., all occur in the FTEA region, with *C. frutescens* being the most widespread; they all display considerable variability in their fruit characters.

Among the characters typical of this genus evident from Figure 15 are the entire leaves; the axillary flowers with distinctive cyathiform, truncate, five-toothed calyces; the campanulate-rotate corollas with five broadly ovate petals; the five equal stamens inserted at the base of the corolla tube; the long filiform styles with small globose stigmas; the bilocular ovaries; and the mature elongate, baccate fruits with somewhat reniform seeds. In *C. annuum* the flowers are solitary becoming pendulous, the calyces are almost entire with five small teeth, the fruits are oblong-ovoid, can be large, and are always pendent, and the seeds smooth as illustrated in Figure 15.

Cyphomandra Mart. ex Sendtn., Flora, 28, 162. 1845. TYPE SPECIES: *Cyphomandra betacea* (Cav.) Sendtn. (*Solanum betacea* Cav.). Figure 16.

Cyphomandra is a predominantly Neotropical rain forest genus of between 30 and 40 species that occur from Mexico to northern Argentina. The species are shrubs, small trees, and vines, and only one, *C. betacea* (Cav.) Sendtn., is found in the FTEA region. Although native to South America, this species, commonly known as the tree tomato, has been widely introduced to many parts of Africa, including Tanzania and Uganda.

Many of the features illustrated in Figure 16 are typical of this genus. They include the large coriaceous leaves; the cymose pendent inflorescence with articulated pedicels; the actinomorphic flowers with cyathiform five-lobed calyces, stellate five-lobed corollas with somewhat triangular spreading petals; the androecium with five connivent anthers ventrifixed to the shorter glabrous filaments; the straight glabrous exserted style; the conical ovary; and the large ellipsoidal baccate fruits with discoid seeds.

Recent work on chloroplast DNA sequence data suggest that *Cyphomandra* should be transferred to the genus *Solanum.* Although Bohs and Olmstead (1994, published 1999) suggested that this genus should not be broken up into smaller monophyletic units until more work on the infrageneric phylogeny of *Solanum* had been done, Bohs (1995) subsequently transferred all *Cyphomandra* species to *Solanum.* Later phylogenetic work based the chloroplast gene *ndh*F sequences (Bohs & Olmstead, 1997) and on cpDNA restriction site variation (Olmstead & Palmer, 1997) verified the previous findings, indicating that both *Cyphomandra* and *Lycopersicon* are derived from within *Solanum*, and that both genera should probably be relegated to subgeneric or sectional status. However, Hunziker (2001) adamantly rejected this treatment, arguing that though closely related, the genera are clearly distinguishable morphologically, and tabulating a number of the delimiting characters. The inclusion of *Cyphomandra* within the genus *Solanum* will be considered during the treatment of the Solanaceae for the *Flora of Tropical East Africa*.

Iochroma Benth., in Edward's Bot. Reg. 30, t. 20. 1845, nom. conserv. emend. descr. TYPE SPECIES: *Iochroma tubulosum* Benth. ("*tubulosa*"), nom. illeg. (*Habrothamnus cyaneus* Lindl., *Iochroma cyaneum* (Lindl.) M. L. Green). Figure 17.

This genus is composed of 15 to 24 woody species of small trees and shrubs that are all native to humid western South America (cf. Hunziker, 1979, 2001); many are of ornamental value owing to their brightly colored corollas. Of these, *I. cyaneum* (Lindl.) M. L. Green and *I. lanceolata* Miers occur both as cultivated plants and as escapes from cultivation in Kenya and Tanzania, and *I. coccineum* Schdw. has been cultivated in Nairobi, Kenya.

Figure 17 illustrates a number of floral characters typical of this genus. They include the conspicuous axillary flowers borne in fascicles; these have urceolate calyces with five shortly triangular lobes, long tubular, shallowly five-lobate corollas, long slender filaments inserted into the basal part of the corolla tube, elongate anthers, a pyriform ovary, and an extremely long filiform glabrous style.

Lycopersicon Mill., Gard. Dict. Abridg. ed. 4. 1754. TYPE SPECIES: *Lycopersicon esculentum* Mill. (*Solanum lycopersicum* L.). Figure 18.

This is a relatively small genus of between six and nine herbaceous, predominantly western South American Andean species that occur from Colombia to northern Chile (cf. Hunziker, 2001). Only *Lycopersicon esculentum* Mill., the tomato, is found throughout the FTEA region, usually as an escape from cultivation. Generic characters visible in the illustration of this species in Figure 18 include the distinctive imparipinnate leaves; the extra-axillary cymose inflorescences with pendent flowers; the five-partite calyx with narrowly elliptic sepals; the stellate five-lobed corollas with strongly reflexed petals; the connivent anthers (borne on very short filaments, which are not shown); the large baccate fruit; and the elliptical seeds. The carpels of this genus are usually bilocular, but in cultivars they are often multi-locular—as illustrated here. Similarly, the anthers are usually conical in such taxa.

The correct generic status of *Lycopersicon* remains the subject of controversy, with authors variously assigning it to *Solanum* or leaving it as a separate genus. D'Arcy (1991) had proposed that the conservation of the name *Lycopersicon esculentum* Mill. over other *Lycopersicon* names for the tomato by the 1987 International Botanical Congress could be construed as support for its separate generic status. Spooner et al. (1993), using data from chloroplast DNA restriction site analysis, concluded that chemical, molecular, and morphological data provided overwhelming evidence for the cladistic relationship of *Solanum* subg. *Potatoe* and *Lycopersicon*. Indeed, Spooner et al. (1993) transferred all *Lycopersicon* epithets to *Solanum*, further proposing the adoption of the epithet *Solanum lycopersicum* L. for the cultivated tomato. Although the chloroplast sequence data later reported by Bohs and Olmstead (1994, published 1999) supported this hypothesis, these authors retained the genera *Lycopersicon* and *Cyphomandra* for the reasons discussed above. However, their subsequent analysis using chloroplast gene *ndh*F sequences (Bohs & Olmstead, 1997) verified that *Lycopersicon* and *Cyphomandra* nested within *Solanum*, while cpDNA restriction site variation strongly indicated that *Lycopersicon* was derived from within *Solanum*, and that it should be relegated to a subgeneric status (Olmstead & Palmer, 1997). Hunziker (2001) again strongly argued against this treatment, considering that *Solanum* and *Lycopersicon* can be clearly differentiated morphologically, and that protoplasmic fusion experiments supported their recognition as distinct genera. The inclusion of *Lycopersicon* as a subgeneric entity of *Solanum* will be considered during the treatment of this genus for FTEA.

Physalis L., Sp. Pl. 182. 1753; Gen. Pl. ed. 5, 85. 1754. TYPE SPECIES: *Physalis alkekengi* L. Figure 19.

Though this genus displays a worldwide distribution, it is predominantly found in the New World with the greatest concentration of species occurring in Mexico and Central America. It is composed of 75 to 100 herbaceous species of which only six have been recorded from the FTEA region, where they are all probably naturalized introductions derived from post-Colombian trading or long-distance dispersal (cf. Symon, 1991). *Physalis peruviana* L. (the Cape gooseberry) and *P. minima* L. occur throughout the area, *P. angulata* L. is found in Kenya and Tanzania, *P. divaricata* L. in Tanzania, and *P. philadelphica* Lam. (the tomate, husk tomato, or tomatillo) in Kenya. However, many of the specimens identified as *P. micrantha* Link have probably been misidentified and could be *P. minima*.

Generic features evident in Figure 19 include the axillary pendent flowers, which are often solitary; the campanulate five-lobed calyx, which greatly enlarges and becomes membraneous in fruit; the broadly campanulate-rotate corollas with five shallow-dentate lobes; and the globose, baccate many-seeded fruit enclosed by the persistent bladdery calyx. The dark (purple) markings in the corolla throat are typical of *P. peruviana* with which *P. edulis* Sims, illustrated in this figure, is synonymous.

Solanum L., Sp. Pl. 184. 1753; Gen. Pl. ed. 5, 85. 1754. TYPE SPECIES: *Solanum nigrum* L. Figures 20–23.

Solanum is one of the largest flowering plant genera occurring in tropical and temperate regions throughout the world. Estimates of the total number of species, which are often called Nightshades, vary between 1000 and 2000, though the accepted number is now thought not to exceed 1400. The genus is considered to be of New World origin, exhibiting its greatest diversity in the Neotropics, particularly in Central and South America. D'Arcy (1991) considered that over 500 *Solanum* species were endemic in the New World. He subdivided the genus into seven subgenera containing approximately 62 sections. D'Arcy (1991) also considered that although expansion of the subgenus *Leptostemonum* (Dunal) Bitter occurred in Africa, only minor centers of diversity evolved there, and that solanaceous diversity in Africa and Madagascar is restricted to sections of the genus *Solanum,* some of which are distinctive and endemic to this region.

Native African *Solanum* species found outside the tropical East African region include *Solanum* subg. *Lyciosolanum* Bitter, which is represented by a single species in extreme southern Africa (D'Arcy, 1991; Jaeger & Hepper, 1986). Various other native African species belonging to various sections in the subgenus *Solanum* and the subgenus *Leptostemonum* have also been reported. These include subgenus *Solanum* sect. *Quadrangulare* Bitter, which is apparently represented by a single endemic species in South Africa (Jaeger & Hepper, 1986; Hunziker, 2001); subgenus *Solanum* sect. *Macronesiotes* Bitter, subgenus *Solanum* sect. *Lemurisolanum* Bitter, and subgenus *Leptstemonum* sect. *Croatii* D'Arcy, all of which are represented by little-known and probable endemics in Madagascar (Jaeger & Hepper, 1986; Hunziker, 2001). D'Arcy (1991) also mentioned that distinctive sections of *Solanum* subg. *Minon* Raf. occur in Madagascar. Other authors have not mentioned the occurrence of this subgenus in Africa, while Knapp (pers. comm.) considers subgenus *Minon* to be synonymous with subgenus *Solanum.* Finally, subgenus *Leptostemonum* sect. *Ischyracanthum* Bitter is represented in dry northeast Africa and the subgenus *Leptostemonum* sect. *Nycterium* (Dunal) Bitter by two species native to the Canary Islands (Jaeger & Hepper, 1986).

Solanum species are herbs, shrubs, climbers, or small trees that exhibit considerable morphological diversity and a range of ecological preferences. Jaeger and Hepper (1986) estimated that around 110 *Solanum* species occur in Africa and its adjacent islands, of which some 20% are probably the result of recent introductions—either deliberate or casual. Approximately 70 *Solanum* species plus many infraspecific taxa have been recorded from Tropical East Africa. Of these, native species appear to belong to the three sections *Afrosolanum* Bitter, *Benderianum* Bitter, and *Solanum* of the subgenus *Solanum*, and the six sections *Anisantherum* Bitter, *Melongena* Dunal, *Monodolichopus* Bitter, *Oliganthes* (Dunal) Bitter, *Somalanum* Bitter, and *Torva* Nees of the subgenus *Leptostemonum* (cf. Jaeger &

Hepper, 1986). However, non-native species belonging to other subgenera and many other sections are widely found throughout this area. As with Solanums elsewhere, the taxa are often extremely difficult to delimit; many exhibit considerable infraspecific variation and there is widespread confusion over identification and names. There are a number of species-complexes e.g., the *S. anguivi* Lam. group and the *S. incanum* L. group—both of the subgenus *Leptostemonum,* and the Black Nightshades—of the subgenus *Solanum* sect. *Solanum,* centering around the generic type species, *S. nigrum* L.

Figures 20–23 illustrate many of the features characterizing *Solanum* together with some of the morphological diversity exhibited by species in this large genus. The pedunculate inflorescences bearing usually actinomorphic flowers with pentamerous calyces, corollas and androecia, the typically connivent anthers, filiform styles, bilocular ovaries and baccate many-seeded fruits are clearly evident from all of these figures. The herbaceous habit typical of species in subgenus *Solanum* sect. *Solanum* is evident in the plate of *Solanum nigrum* (Fig. 20), where other sectional characters visible include the simple leaves, the cymose inflorescences, the stellate flowers with recurved petals, the filaments fused to the basal half of the corolla tube, and the connivent anthers dehiscing by apical pores, which become lateral slits. The other three species illustrated belong to subgenus *Leptostemonum* all of which are characterized by stellate trichomes, which are often modified to form prickles, as shown in Figures 21 and 23. The cymose inflorescences in this subgenus vary from being simple and relatively few-flowered as in *S. anguivi* (Fig. 22) and *S. incanum* (Fig. 23) to multiple-branched and many-flowered as in *S. giganteum* Jacq. (Fig. 21). These latter three species belong to the sections *Oliganthes* (Dunal) Bitter, *Melongena* (Mill.) Dunal, and *Torva* Nees, respectively.

Many of the species are important food plants, e.g., the potato, *S. tuberosum* L.; the African eggplants, *S. aethiopicum* L., *S. gilo* Raddi, *S. macrocarpon* L., and *S. melongena* L.; and the African nightshades, *S. nigrum* sensu lato. Others are cultivated as ornamentals, either for their showy flowers, e.g., the Jasmine Nightshade, *S. jasminoides* Paxton, or for their colorful berries, e.g., the Jerusalem cherry, *S. pseudocapsicum* L. The genus is also a source of toxins—largely in the form of steroidal alkaloids such as solanidane; of medicinal drugs with *S. incanum*, for example, being one of the most widely used African medicinal species; and of drug precursors such as solasodine used in the production of corticosteroids and which is found in around 200 *Solanum* species (cf. Hawkes, 1999). A number of species figure prominently in ethnobotanical practices throughout the FTEA region. Indeed, Bukenya and Carasco (1999) reported that most of the 27 *Solanum* species found in Uganda play important social and economic roles among local populations, being used for magic, spiritual rites and fertility cults as well as for food, medicine, and ornamentals.

Withania Pauquy, Diss. Bellad., 14. 1825, nom. cons. TYPE SPECIES: *Withania frutescens* (L.) Pauquy (*Atropa frutescens* L.) (typ. cons.). Figure 24.

This genus is indigenous to the Old World and is found throughout Africa and the warmer parts of Asia. Hepper (1991) considered that *Withania* was composed of 10 species of perennial herbs or semi-woody shrubs of dry areas, though up to 20 species have been described. Hunziker (cf. 2001) has recently enlarged this genus by adding nine mesophytes formerly included in the genera *Mellissia* Hook. and *Physaliastrum* Makino on the basis of the ventrifixed anthers, accrescent calyces, and embryo structure. The 18 species that Hunziker now includes in *Withania* would extend the geographical range of this genus from the Canary Islands in the west, through Asia to China and Japan in the east. However, Hunziker (2001: 269) stated that this treatment "simplifies the taxonomy of the Asiatic Solanaceae at least until these plants are better studied and more information becomes available."

Withania is one of only two solanaceous genera that D'Arcy (1991) considered to be truly African and which Symon (1991) considered to be a distinctive African Gondwanan element. Only *W. somnifera* (L.) Dunal seems to occur in tropical East Africa, where it is widespread in all three countries, and from where it extends across the continent to the Mediterranean and tropical Asia. Hepper (1991) speculated that the frequency of this weed in the warmer, drier countries may be due to its use as a minor medicinal plant.

Many of the generic features distinguishing *Withania* are illustrated in Figure 24. They include the axillary flowers borne in fascicles on short pedicels; the campanulate five-toothed calyces that become enlarged in fruit; the campanulate corollas with five long, narrowly triangular petals; the stamens inserted at the base of the corolla tube with short filaments; the relatively short filiform style and the globose baccate fruits with many reniform reticulate seeds. The striking elongations to the calyx segments in this figure are typical of *W. aristata* Pauq.

DISCUSSION

It is probable that East Africa embraces the largest number of solanaceous species found on the continent of Africa. From this overview, it also seems probable that of the 21 genera represented in tropical East Africa, only 4, namely *Discopodium*, *Lycium*, *Solanum,* and *Withania,* embrace species which are endemic to both this region and Africa as a whole, and that of these only *Discopodium* and *Withania* are distinctive African genera. Moreover, as expected, the genus *Solanum* is represented by the largest number of species, including both endemic and introduced taxa. Even within this genus, however, there is now some evidence that species in *Solanum* subg. *Leptostemonum* originated and initially diversified in South America before dispersal to Africa where subsequent divergence then occurred (cf. Olmstead & Palmer, 1997). On the basis of their cpDNA restriction site variation analysis Olmstead and Palmer (1997) suggested that the low level of cpDNA divergence among African, Australian, and the most closely related American species could not be explained by continental drift, but indicated that dispersal to Africa was probably across a much narrower Atlantic Ocean. There is also little doubt, again as expected, that within the family, these *Solanum* species show the greatest taxonomic complexity and that their relationships will prove the most difficult to resolve. The remaining 17 genera represented in this region were probably introduced, either deliberately for their economic or gastronomic value, or accidentally, especially during the intensive travel and trading that followed the discovery of the Americas by the Europeans. Most of these species have originated from the Neotropics, particularly from Central and South America. Many of the species have successfully established themselves as adventive or casual taxa throughout all three countries—often as escapes from cultivation. The widespread cultivation of many of these solanaceous species has been due not only to their importance as food plants, but also to their value as ornamentals and as sources of drugs and medicines. Solanaceous plants have been widely used medicinally since the dawn of civilization (Roddick, 1991). Most of the genera found in Tropical East Africa undoubtedly play important socio-economic roles in both rural and urban communities.

It is perhaps fitting that I have referred predominantly to papers published in the Solanaceae International Conference Series, with which Bill D'Arcy was so involved. From these volumes and the bibliographies of the papers cited by their authors, it is clear that an enormous amount of research encompassing many different disciplines has been stimulated since the inception of these Conferences in 1976. This work, together with that currently in progress, has and will continue to elucidate systematic and phylogenetic relationships at all taxonomic levels within the family, and will undoubtedly be of considerable interest and use during the revision of the Solanaceae for the *Flora of Tropical East Africa*.

ACKNOWLEDGMENTS

It was a great privilege to be asked to contribute a paper to this memorial volume. Although I only met Bill D'Arcy once, at the first Solanaceae Conference in 1976, I greatly appreciated his advice and encouragement during our lengthy correspondence on various problems associated with *Solanum* sect. *Solanum*, especially during my early days as a rather naïve Solanologist.

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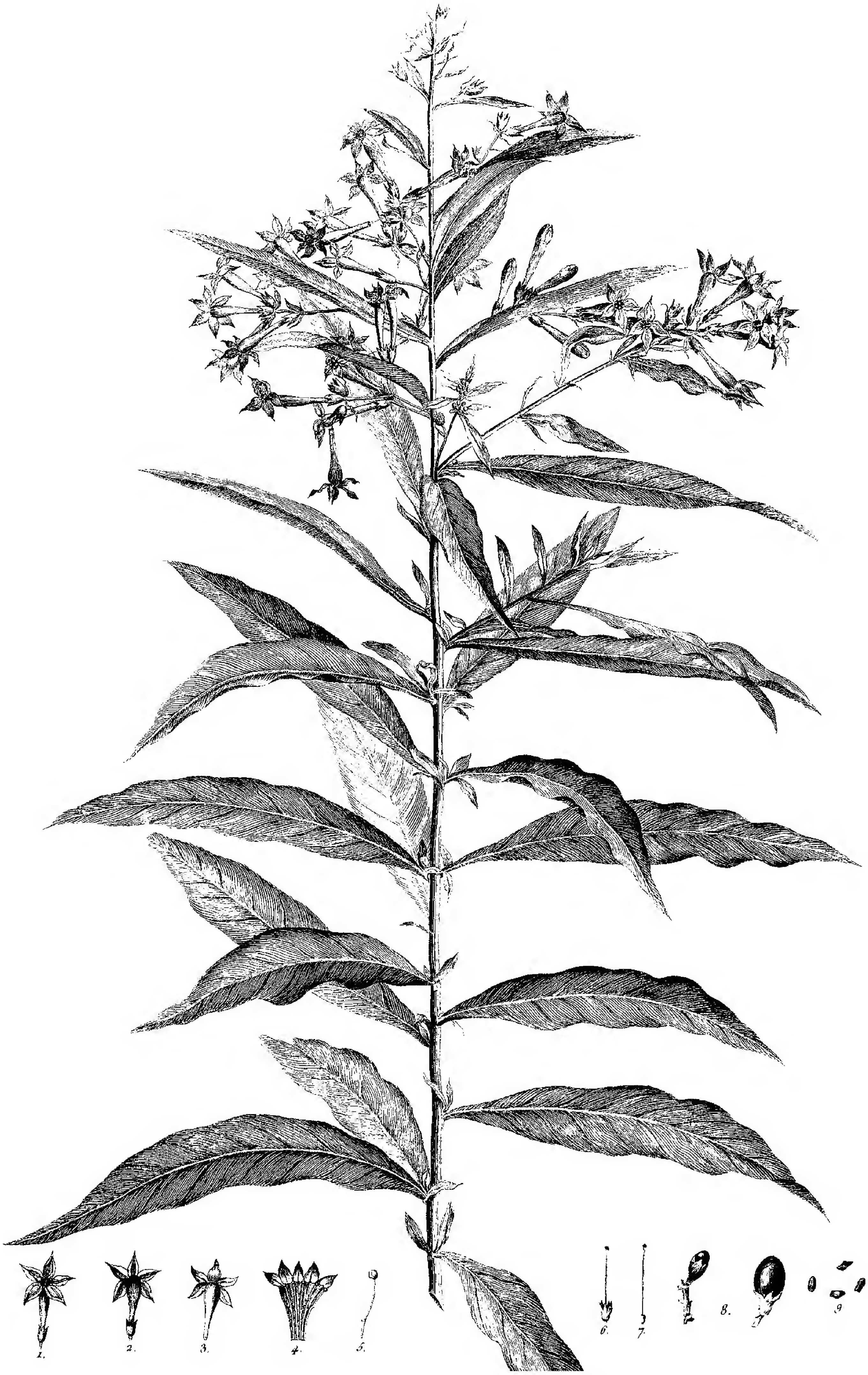

Figure 1. *Cestrum parqui* L'Hér.—from L'Héritier, Stirp. Nov., Fasc. 4, pl. 36. 1788.

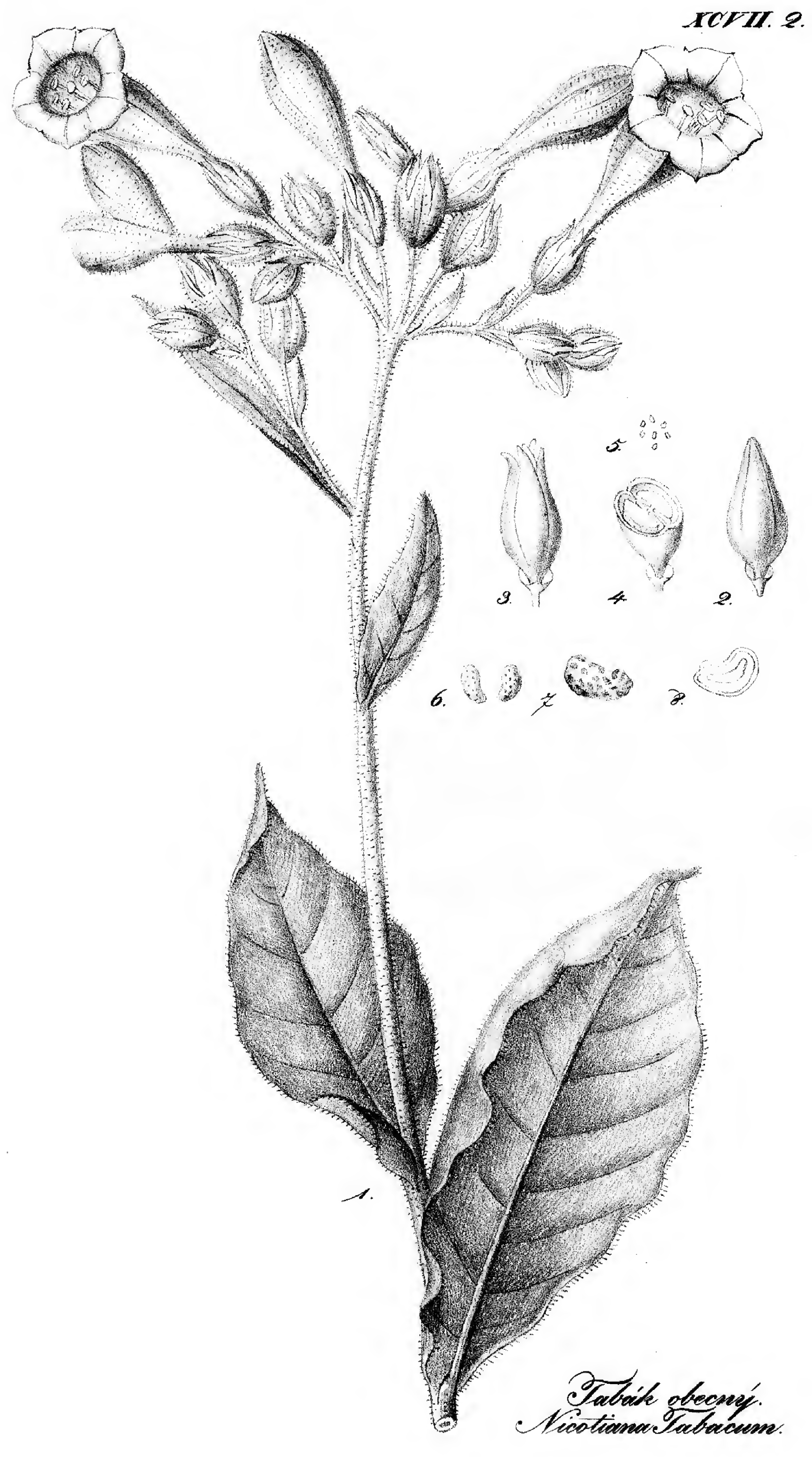
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Figure 2. *Nicotiana tabacum* L.—from Berchtold & Presl, Rostlinar 1, t. 45. 1823.

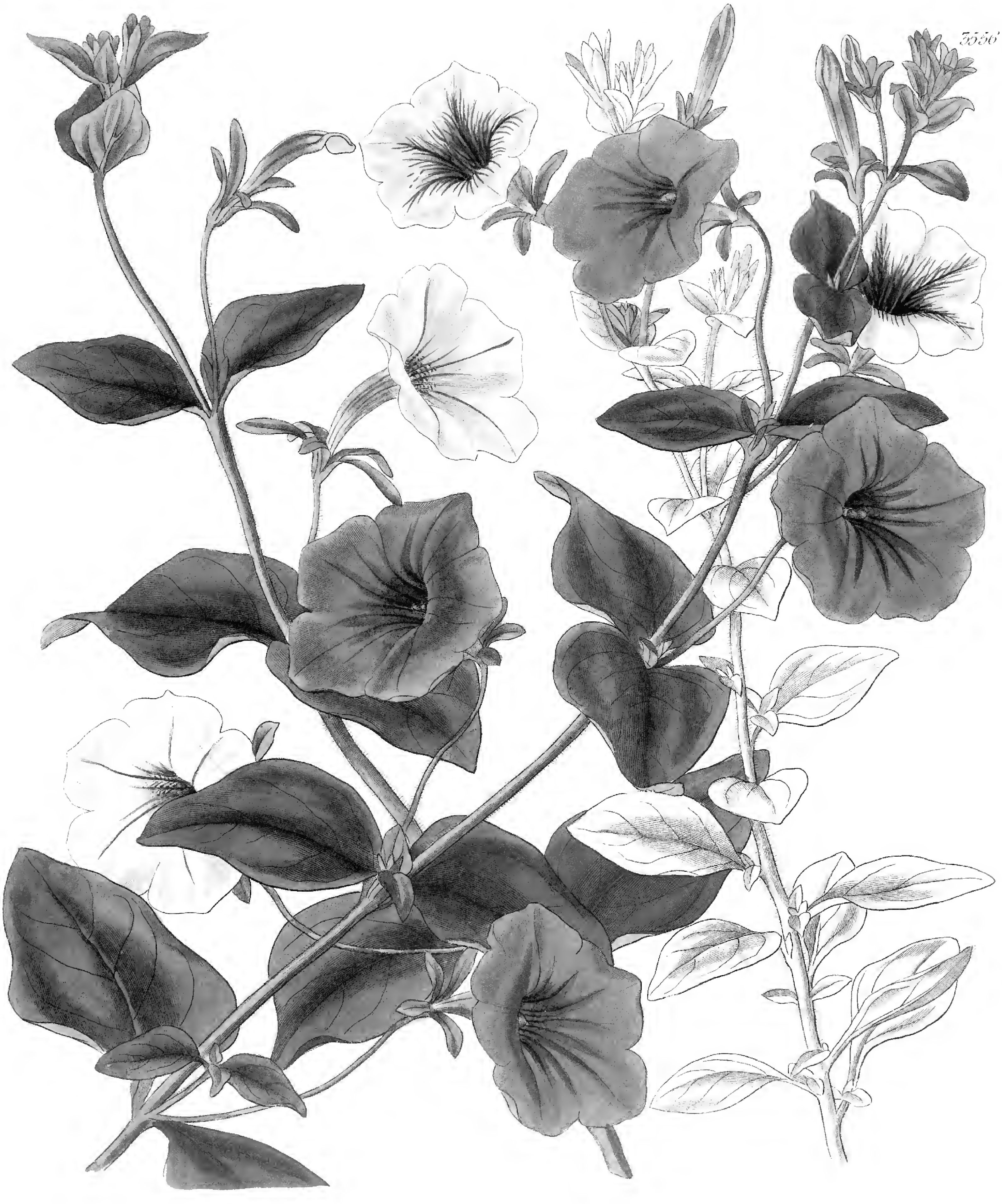


Figure 3. *Petunia violacea-hybrida* Hook.—from Curtis's Bot. Mag., 64, t. 3556. 1837.

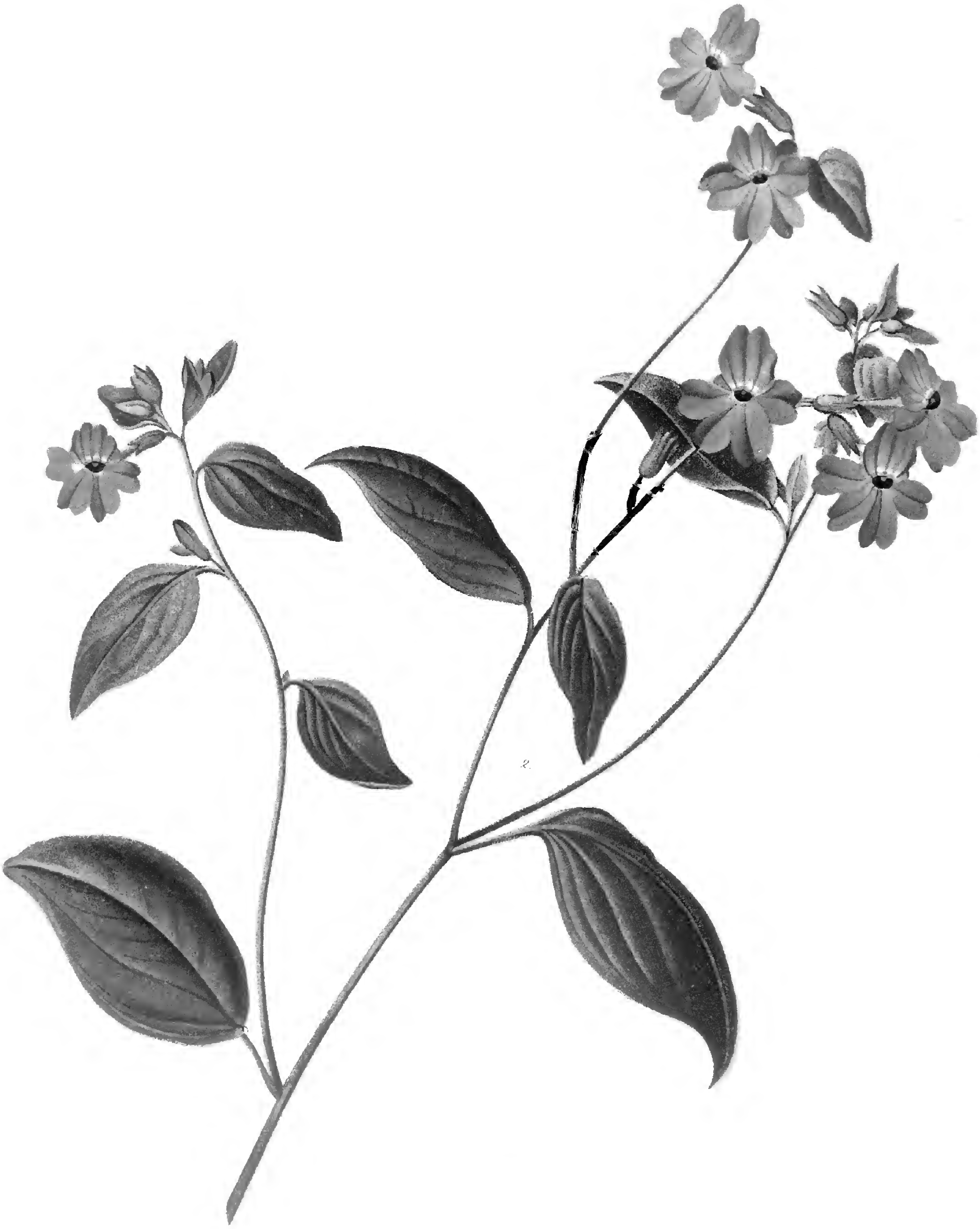
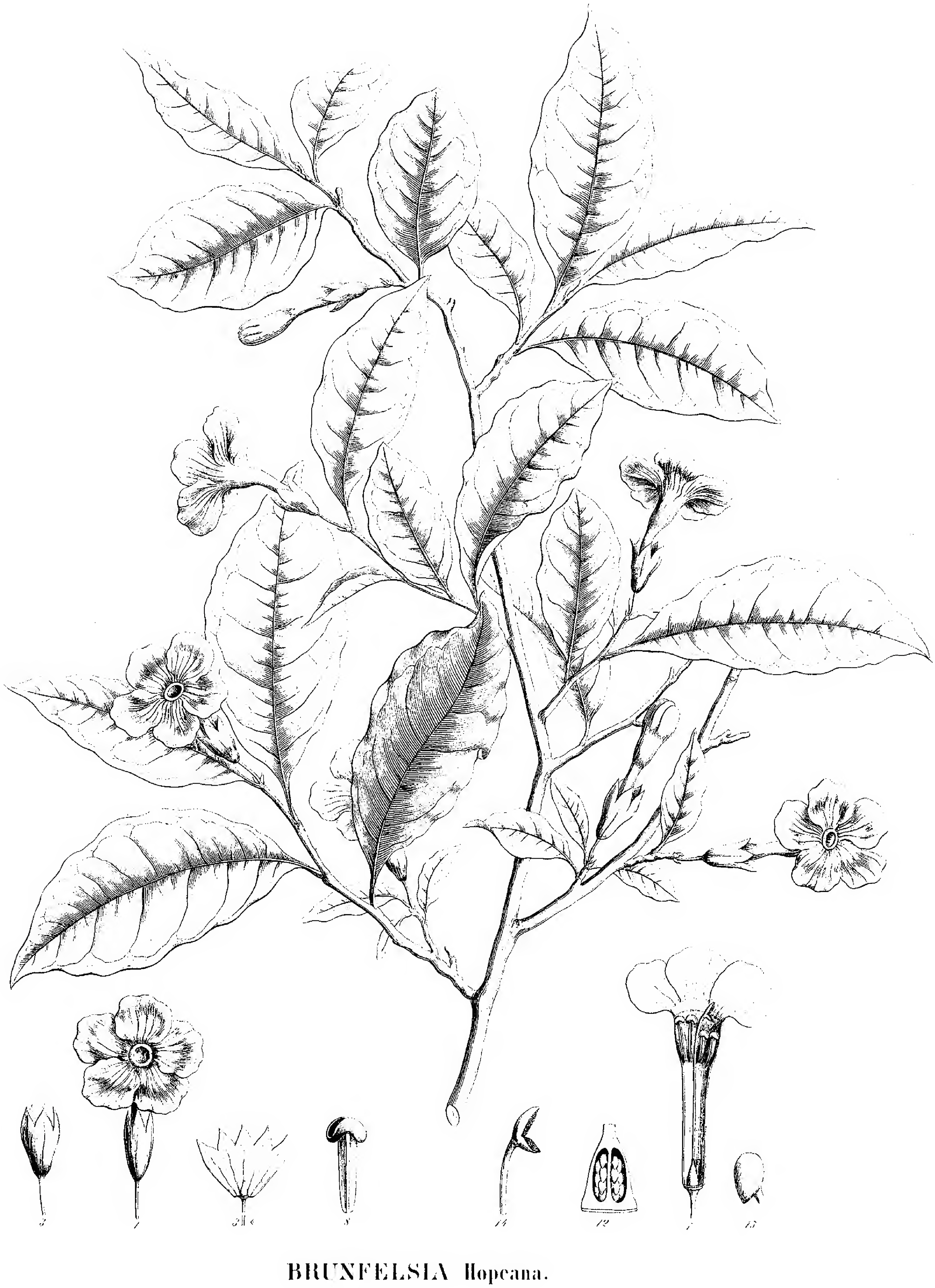


Figure 4. *Browallia viscosa* HBK—from Regel Gartenflora, 4, t. 142. 1855.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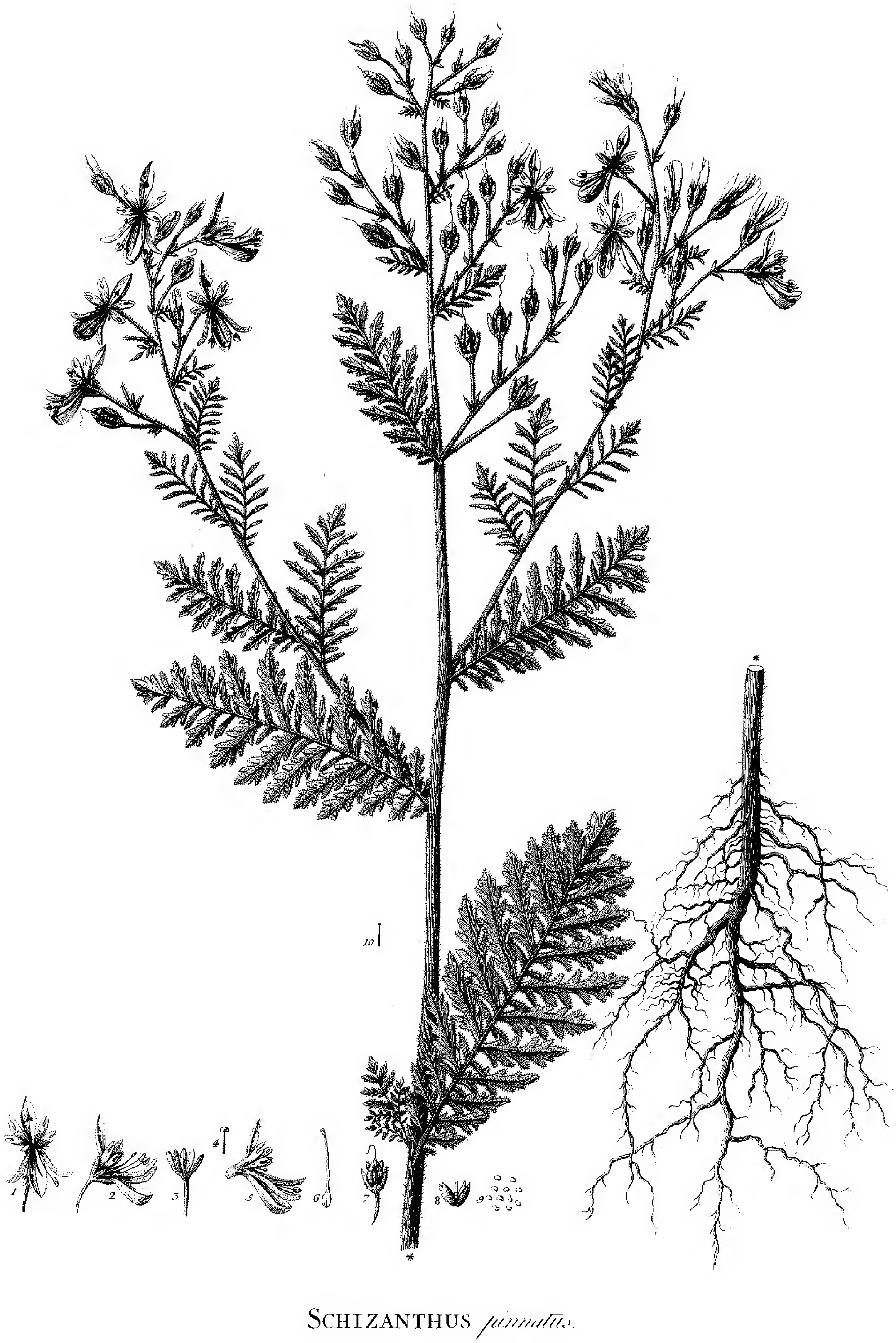
BRUNFELSIA Hopeana.

Figure 5. *Brunfelsia hopeana* Benth.—from Martius, Fl. Bras., 8, t. 43. 1862.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SCHIZANTHUS pinnatus.

Figure 6. *Schizanthus pinnatus* Ruiz & Pav.—from Ruiz & Pavón, Fl. Peru. & Chilensis, 1, t. 17. 1798.

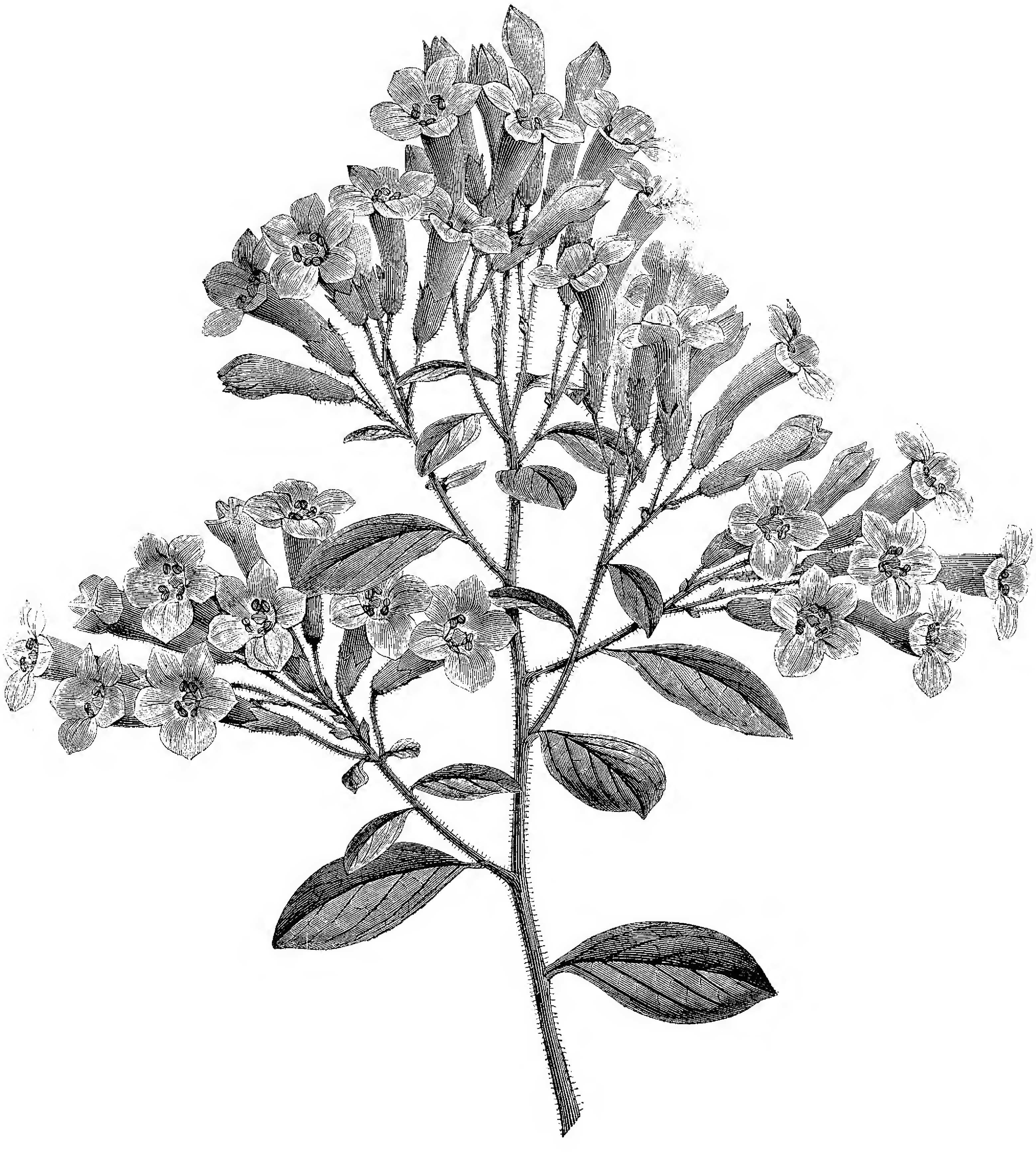

Figure 7. *Streptosolen jamesonii* (Benth.) Miers—from Gard. Chronicle 21: 797, fig. 147. 1884.

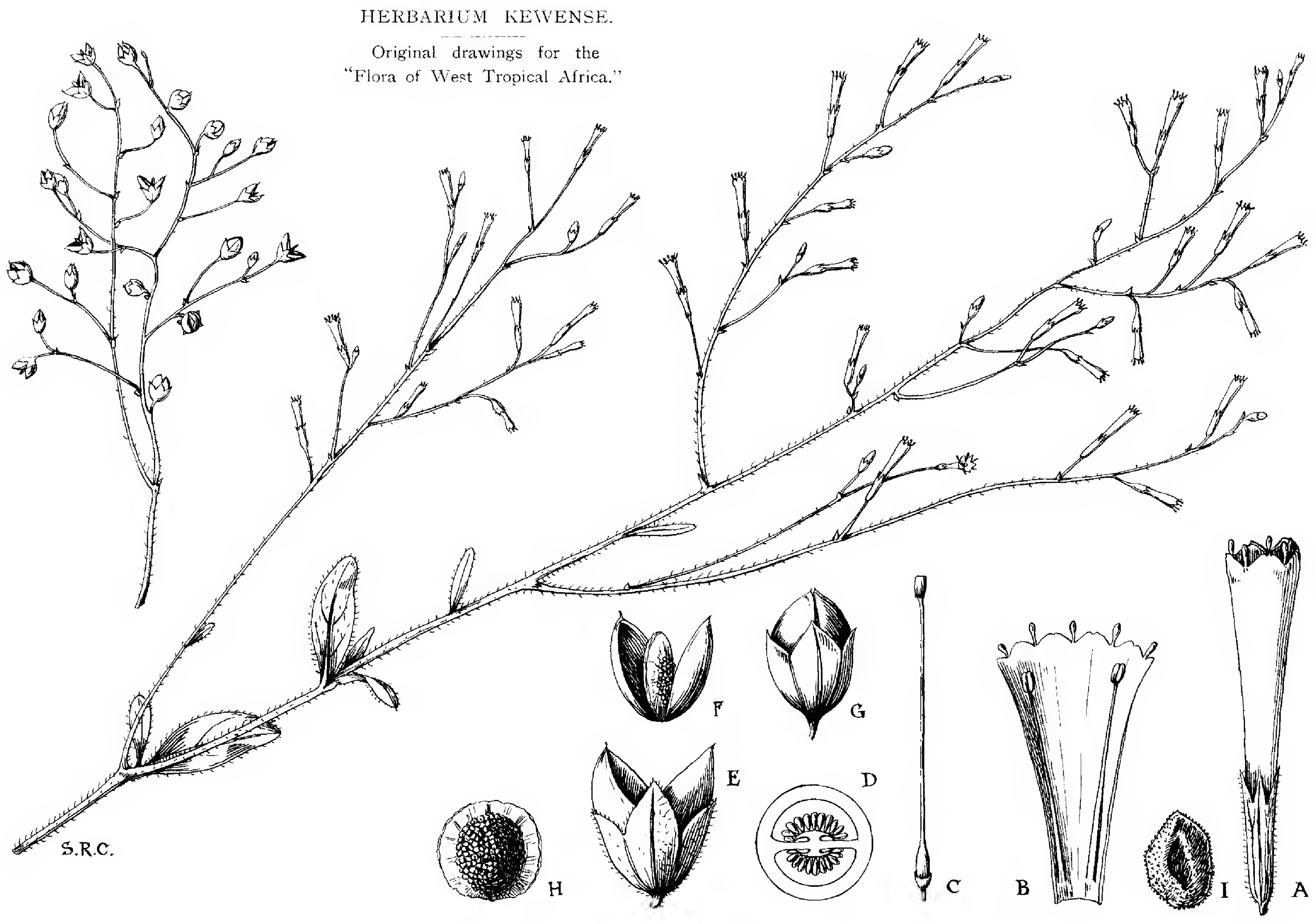
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Figure 8. *Schwenckia americana* L.—from Hutchinson & Dalziel, Fl. W. Trop. Afr. 2: 327, fig. 279. 2nd ed. 1963. (Ed. F.N. Hepper). Reproduced by kind permission of Stella Ross-Craig.

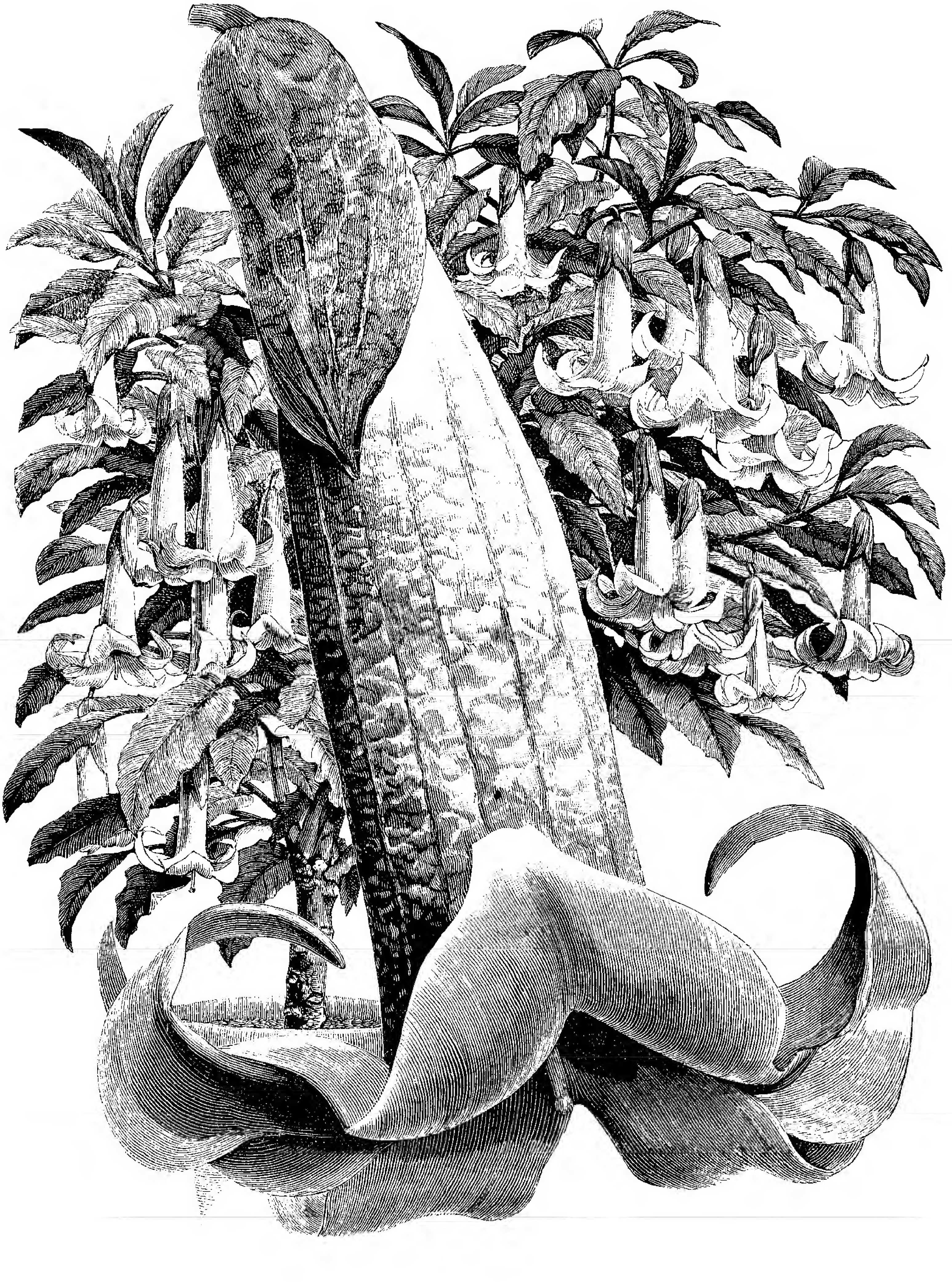

Figure 9. *Brugmansia arborea* (L.) Lagerh.—from J. Hort. Ser. 3, 40: 201. 1900.

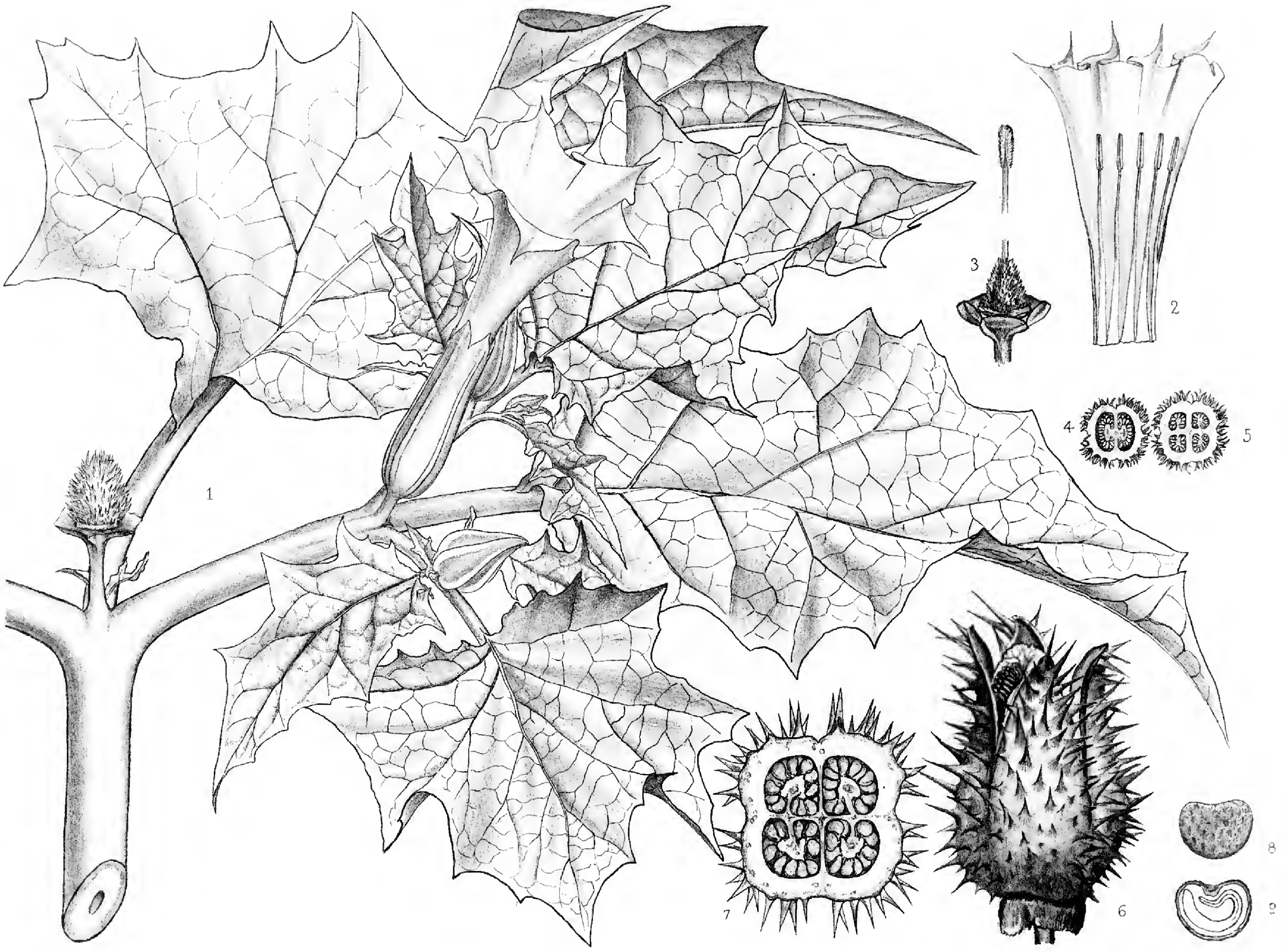

Figure 10. *Datura stramonium* L.—from Bentley & Trimen, Medicinal Plants 3: 192. 1880.

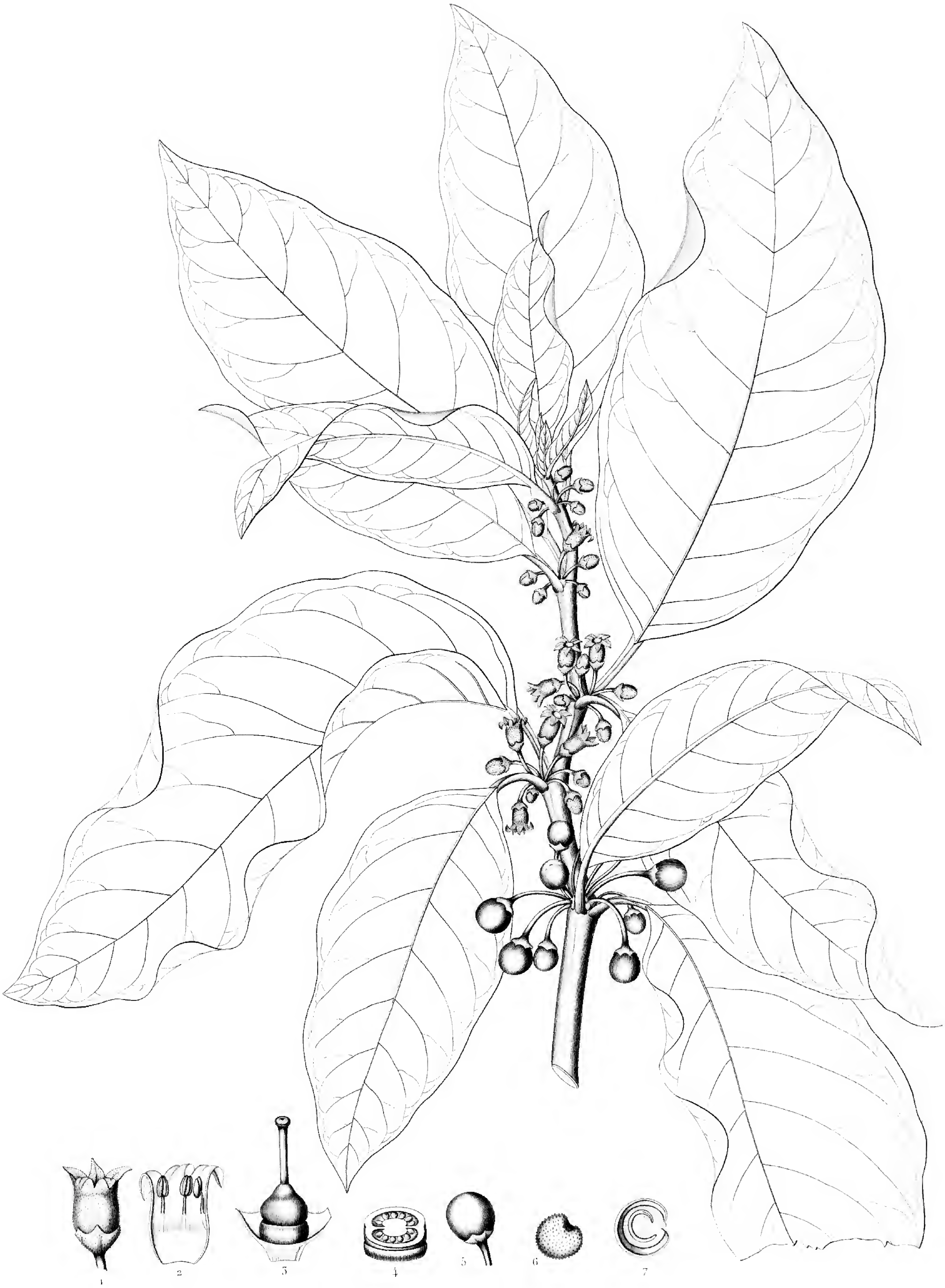

Figure 11. *Discopodium penninervium* Hochst.—from Richard, Tent. Fl. Abyssin. Atlas, pl. 79. ?1851.

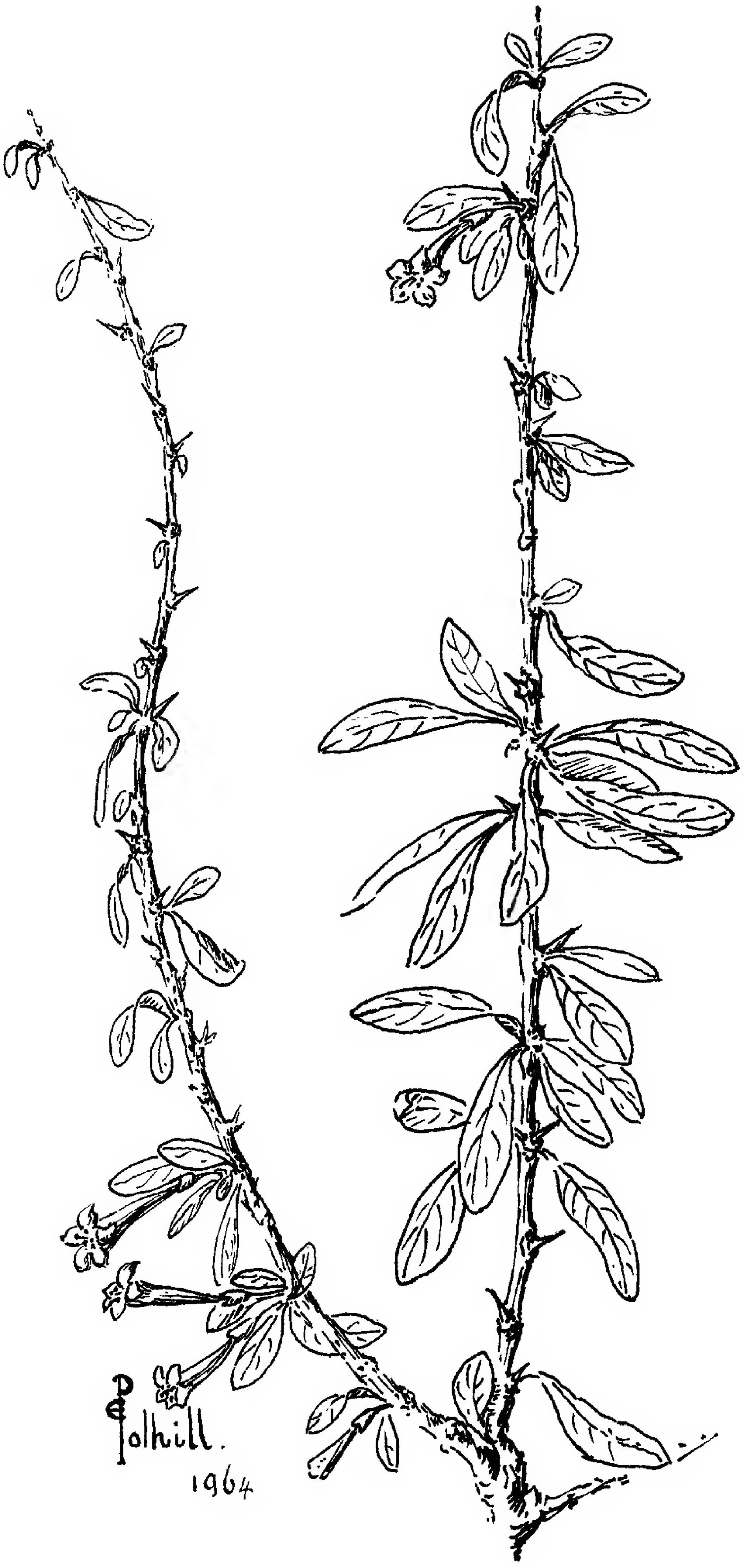

Figure 12. *Lycium europaeum* L. (= *L. shawii* Roem. & Schult.). Painting by Evelyn Davidson Polhill (1964). (RBG, Kew Collection.)

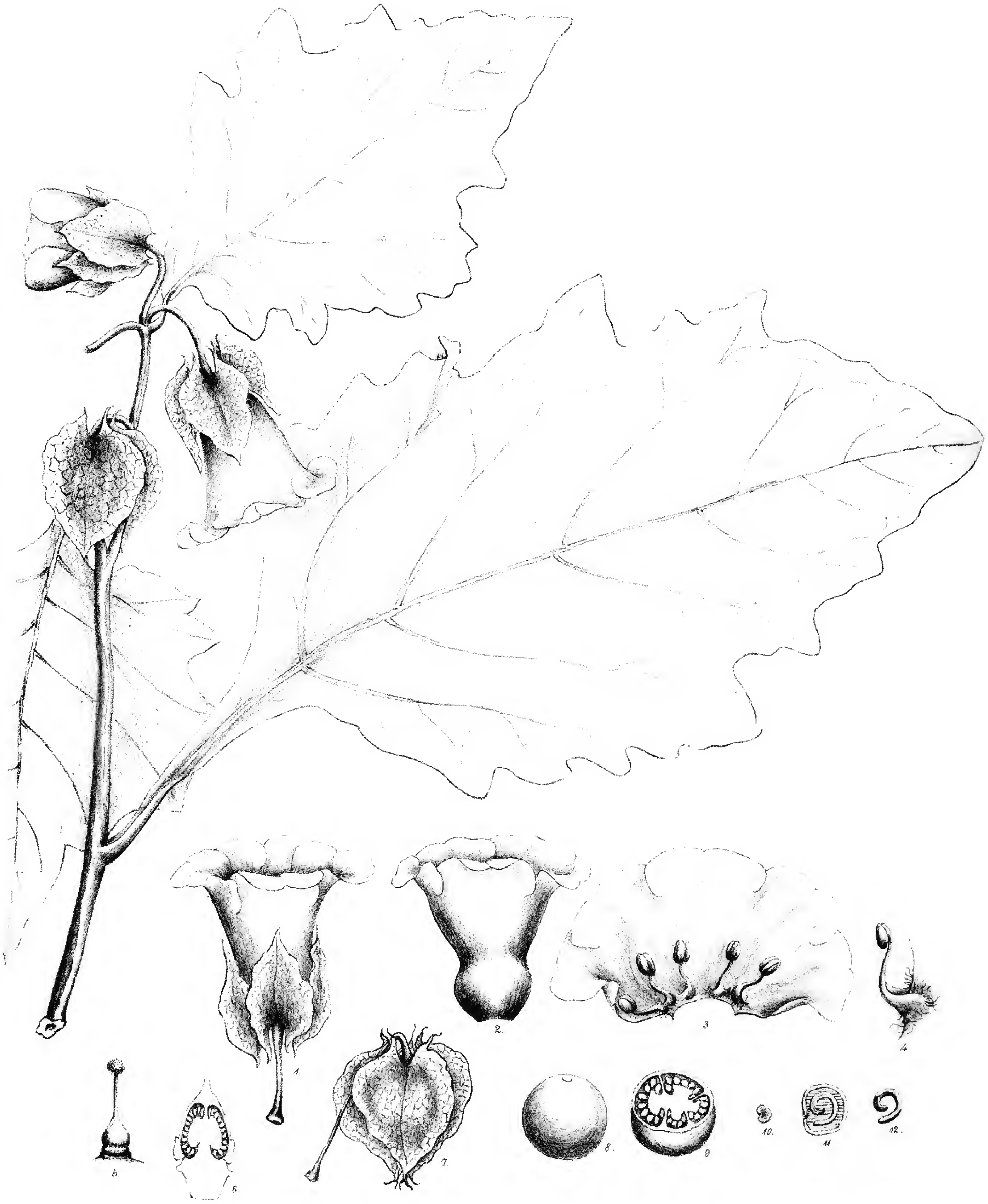
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Figure 13. *Nicandra physalodes* (L.) Gaertn. ("*physaloides*")—from Miers, Illustr. S. Am. Pl., 2, pl. 43. 1849.

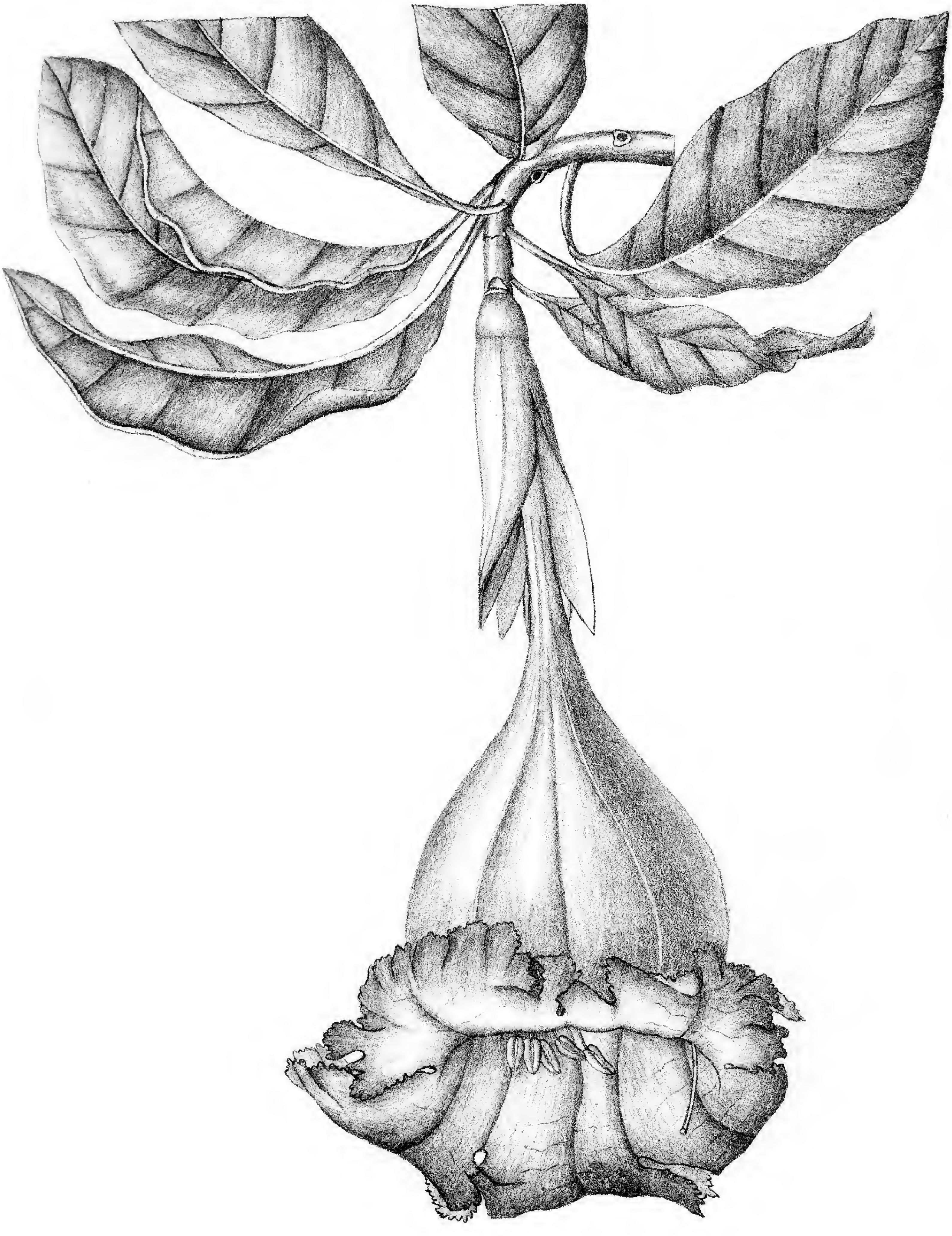

Figure 14. *Solandra grandiflora* Sw.—from Berchtold & Presl, Rostlinar, 1, t. 54. 1823.

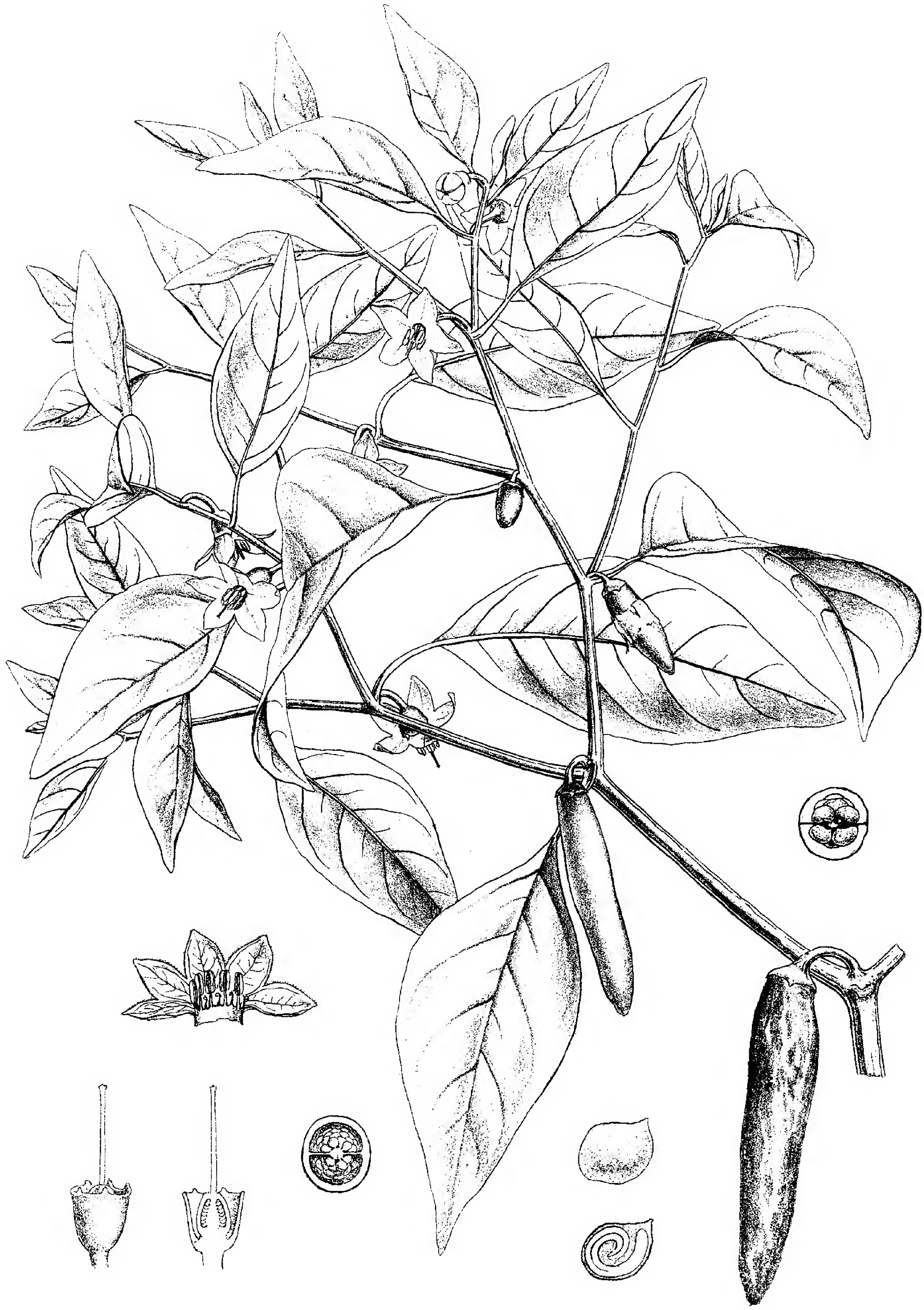

Figure 15. *Capsicum annuum* L.—from Bentley & Trimen, Medicinal Plants 3: 189. 1880.

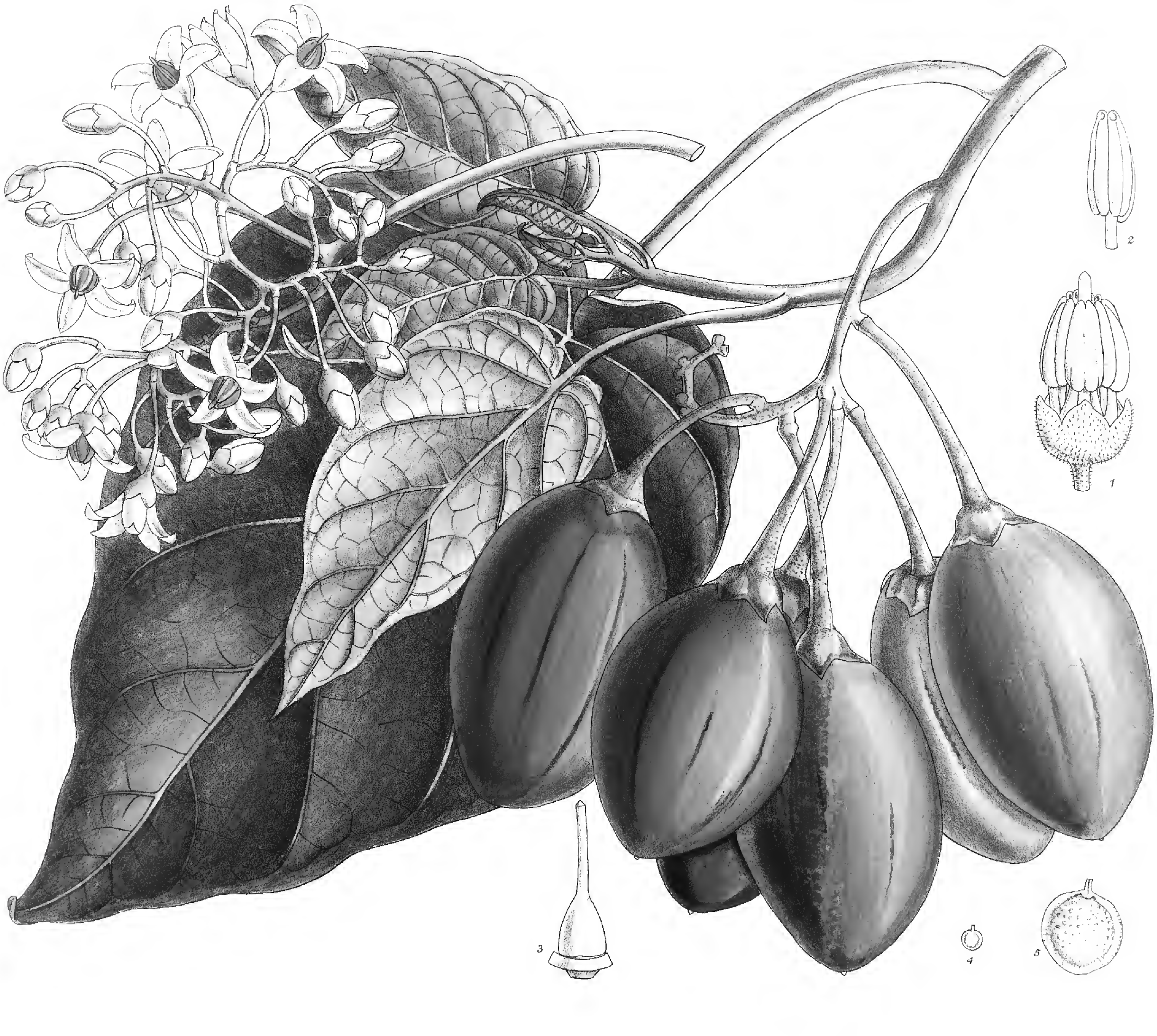

Figure 16. *Cyphomandra betacea* (Cav.) Sendtn.—from Curtis's Bot. Mag., 125, t. 7682. 1899.

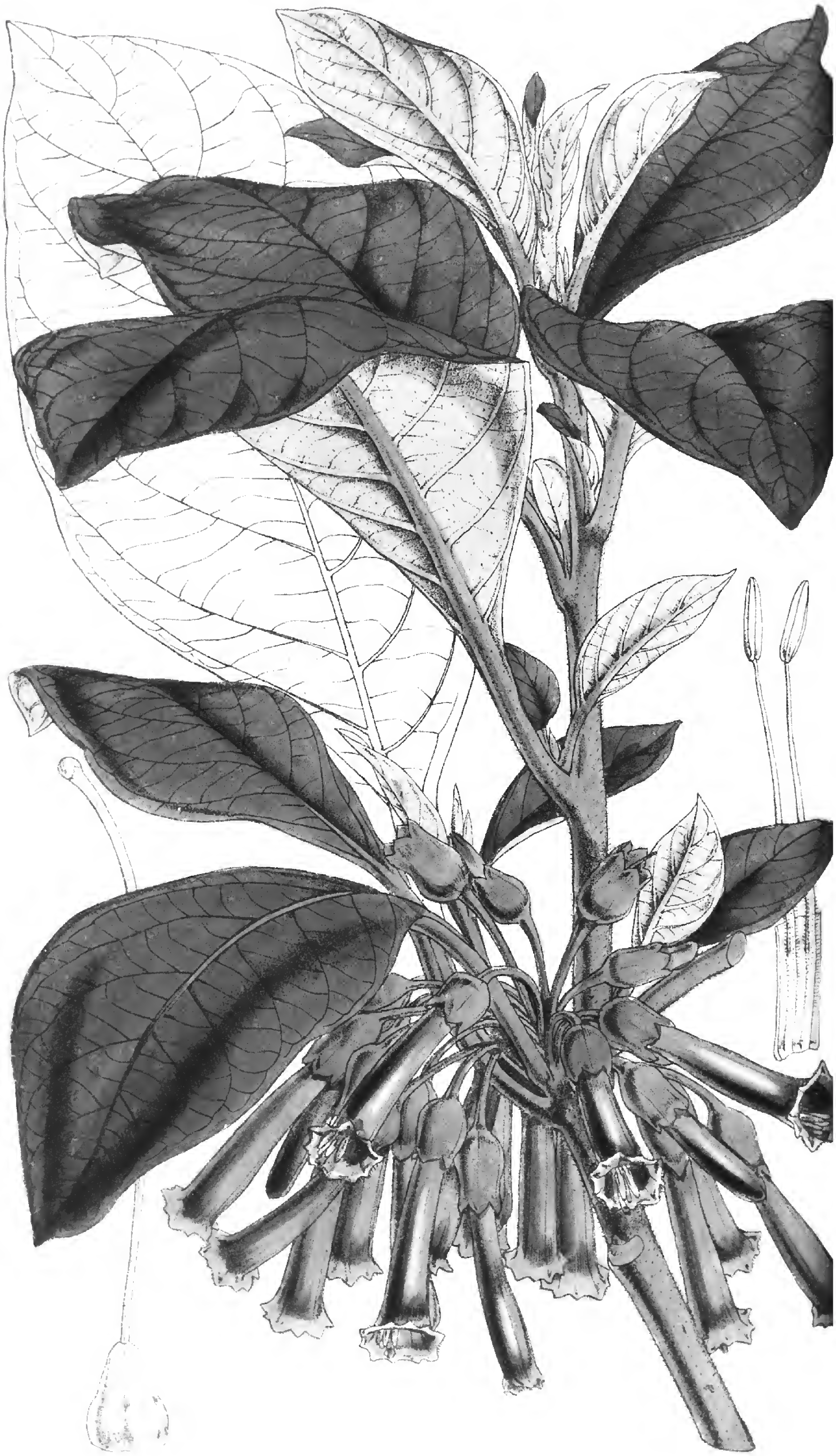

Figure 17. *Iochroma lanceolata* Miers—from Curtis's Bot. Mag., 73, t. 4338. 1847.

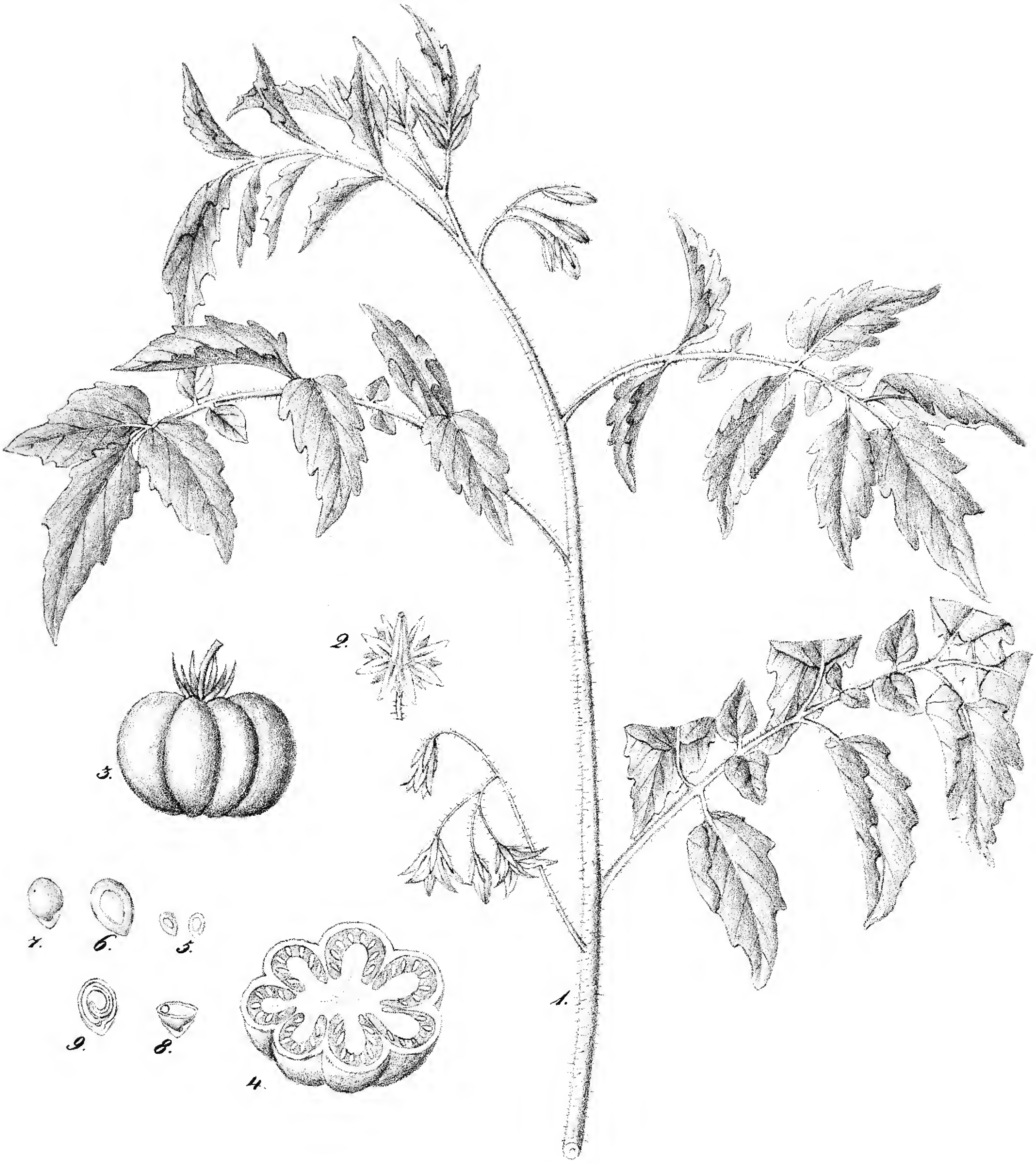

Figure 18. *Lycopersicon esculentum* Mill.—from Berchtold & Presl, Rostlinar. 1, t. 49. 1823.

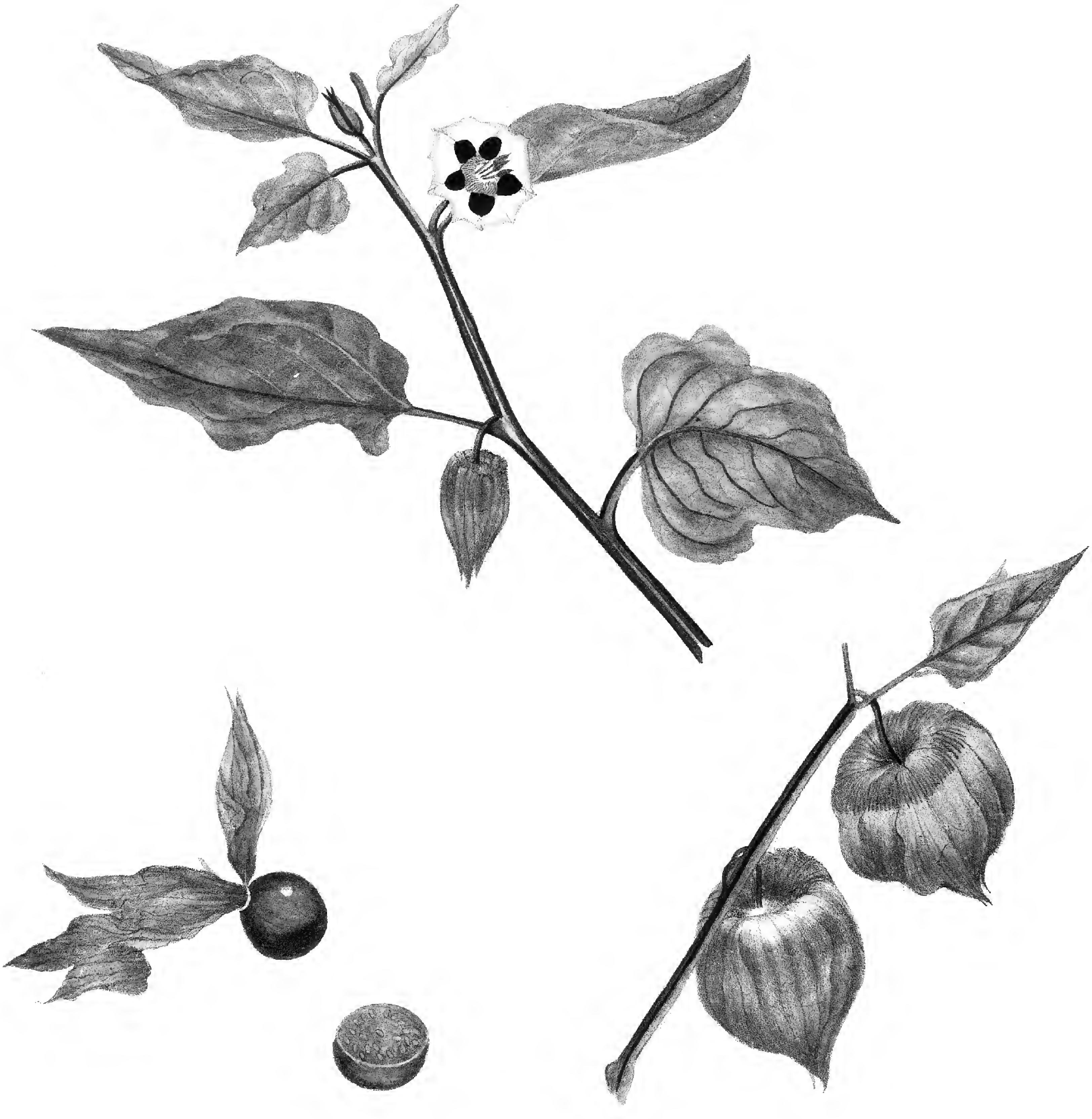

Figure 19. *Physalis edulis* Sims (= *P. peruviana* L.)—from Penfold, Madeira: Flowers, Fruits & Ferns, pl. 11. 1845.

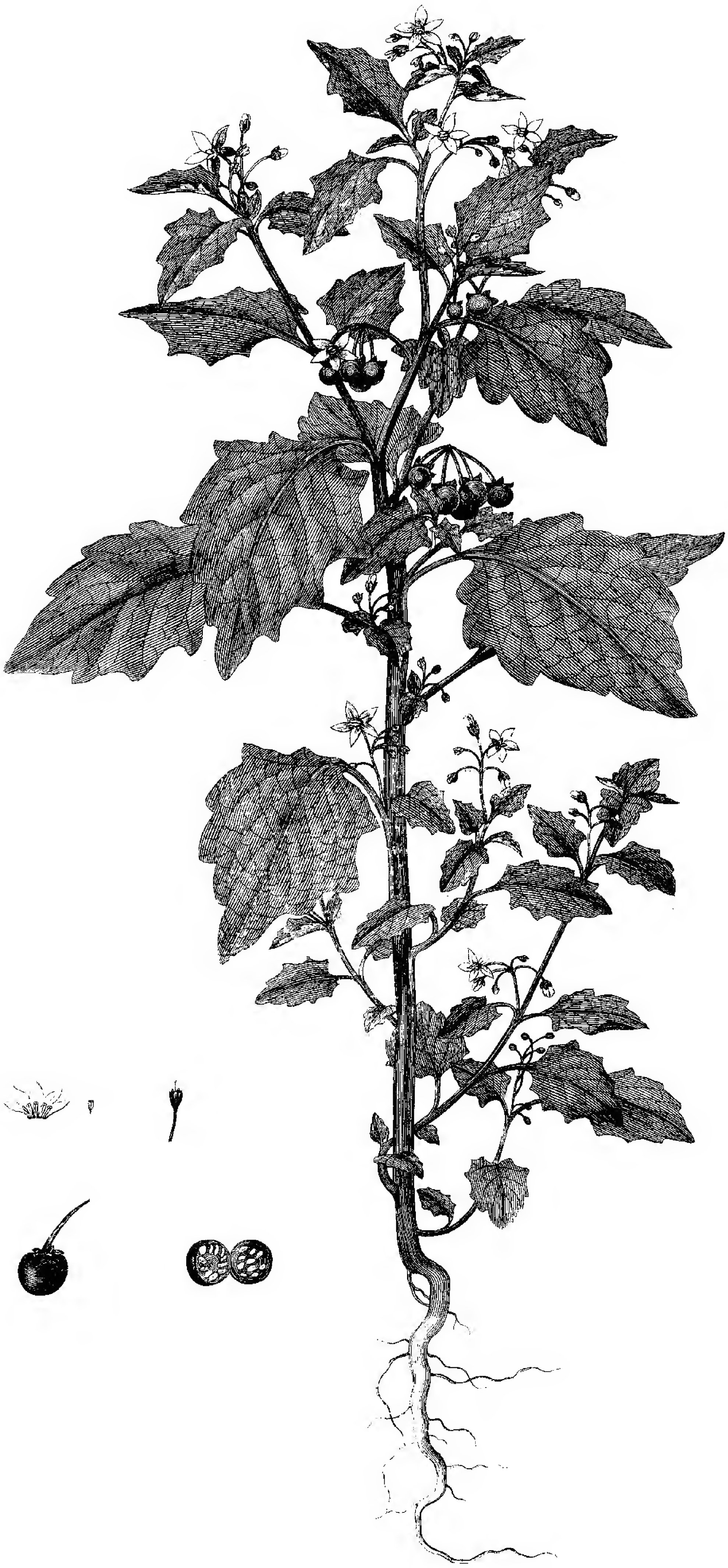

Figure 20. *Solanum nigrum* L.—from Oeder, Flora Danica 3, t. 460. 1769.

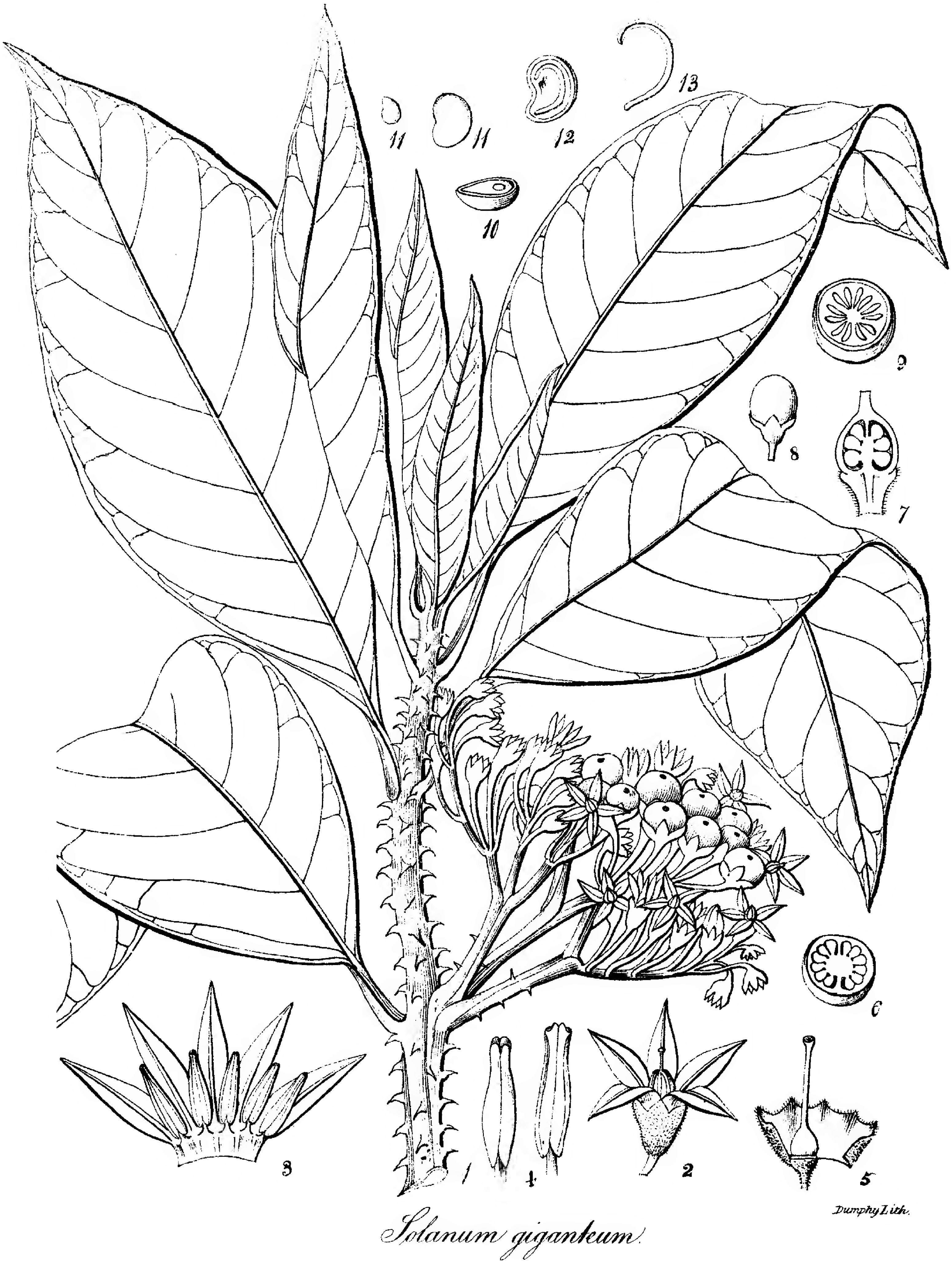
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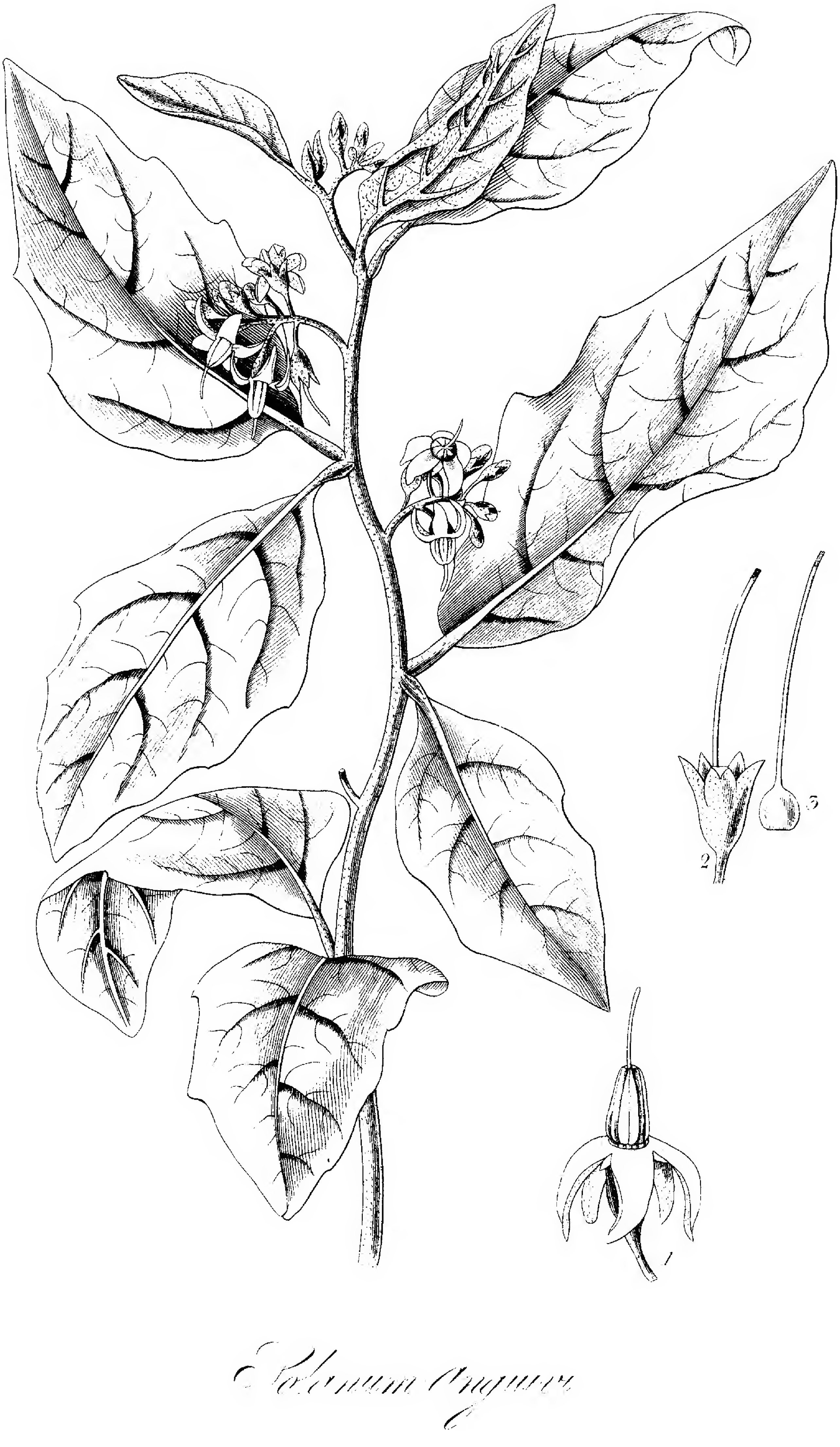
Figure 21. *Solanum giganteum* Jacq.—from Wight, Ic. Pl. Ind. Or., 3, t. 893. 1843.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Solanum Anguivi

Figure 22. *Solanum anguivi* Lam.—from Hooker, Exot. Fl. 3, t. 199. 1826.

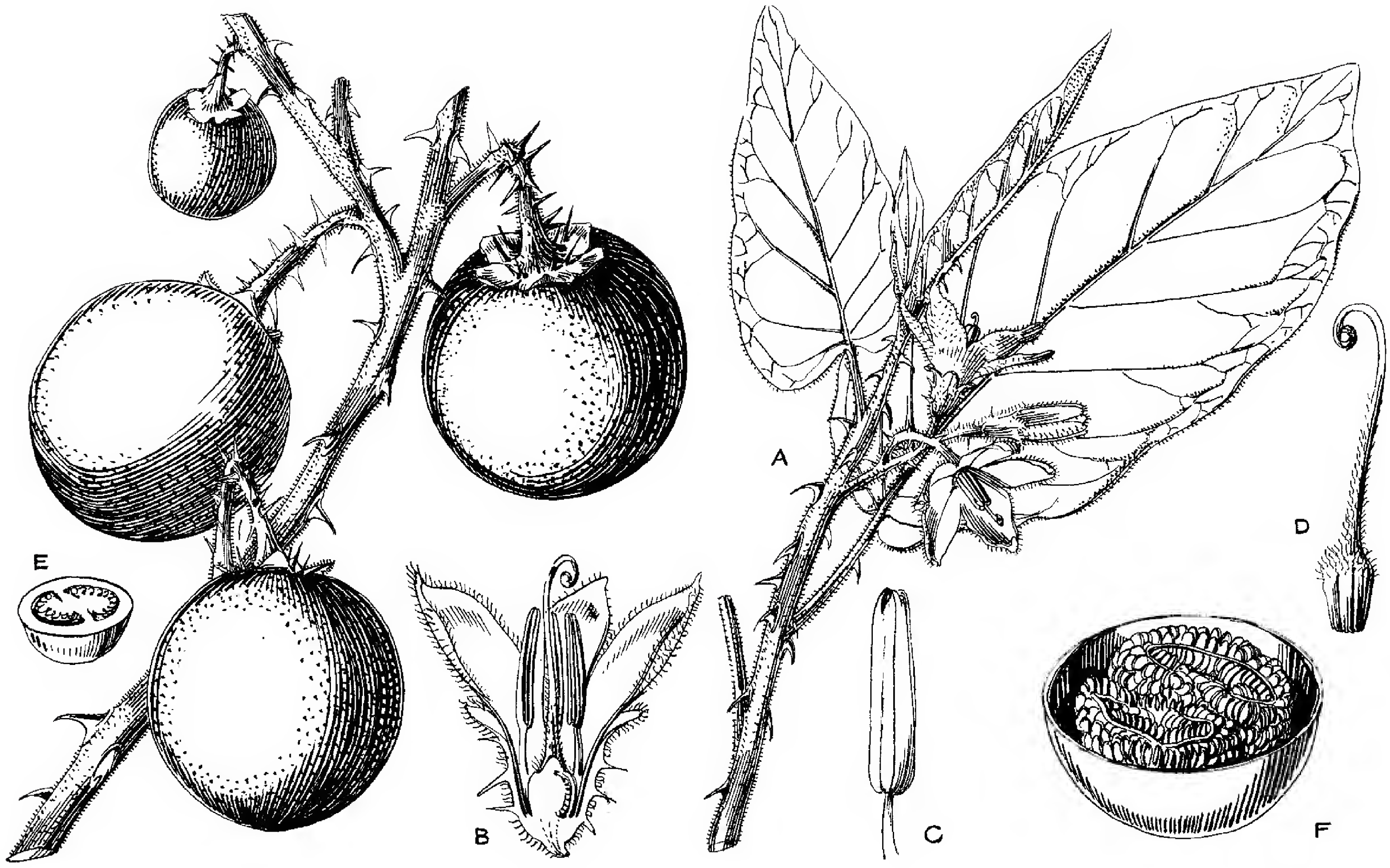

Figure 23. *Solanum incanum* L.—from Hutchinson & Dalziel, Fl. W. Trop. Afr. 2: 333, fig. 281 (2nd ed., Ed. F. N. Hepper). 1963.

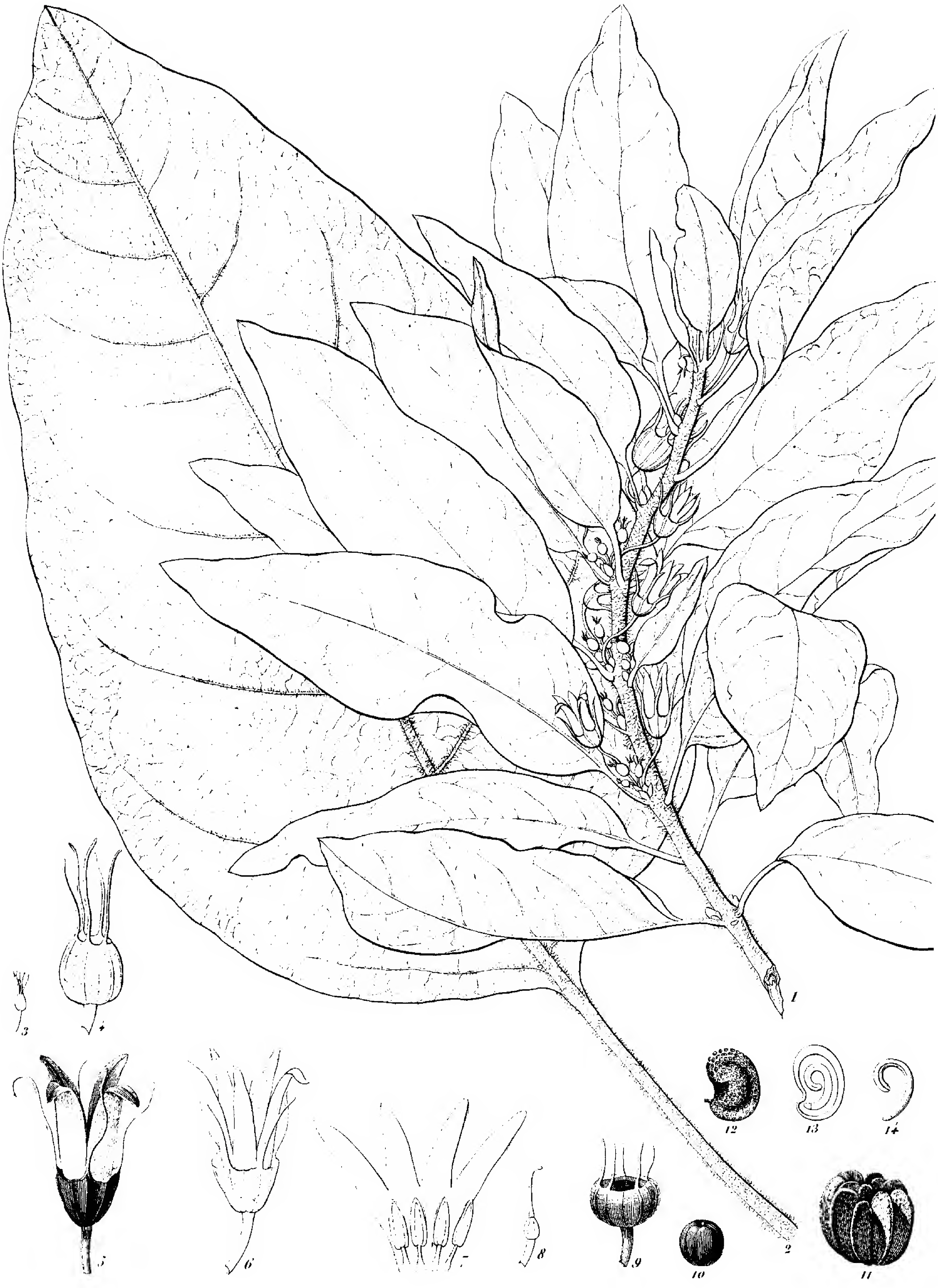
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Figure 24. *Withania aristata* Pauq.—from Webb & Berthelot, Hist. Nat. Iles Canaries: 2nd Part, Phytogeographie canar., 3, t. 175. 1844–1850.

BIOLOGY AND CHARACTERS USED IN SOLANACEAE

9

TAXONOMY OF MEXICAN DIPLOID WILD POTATOES (*SOLANUM* SECT. *PETOTA*): MORPHOLOGICAL AND MICROSATELLITE DATA

Sabina I. Lara-Cabrera and David M. Spooner

Abstract. *Solanum* sect. *Petota*, the potato and its wild relatives, contains about 200 wild species distributed from the southwestern United States to central Argentina and adjacent Chile. Most species grow in the Andes, but the United States, Mexico, and Central America contain about 30 diploid ($2n = 24$) taxa, as well as tetraploid ($2n = 48$) and hexaploid ($2n = 72$) ones. Chloroplast DNA restriction site data showed 13 of these 30 taxa to form a clade containing only diploid species, but there was low resolution within the clade. Some of these 13 taxa are similar morphologically, and we questioned whether they were valid species. We analyzed these and related taxa with morphological and microsatellite data. Morphological data showed extensive overlap of putative species-specific characters, but most species could be supported by multivariate techniques, except *S. brachistotrichium* and perhaps *S. stenophyllidium*. Previously mapped nuclear microsatellite markers, developed in *S. tuberosum*, also were explored for help to define species but performed poorly, showing that these microsatellites have reduced phylogenetic utility to analyze the United States, Mexican, and Central American diploid wild potato species.

Key words: microsatellite, potato, simple sequence repeats, *Solanum* sect. *Petota*, SSR.

Solanum sect. *Petota* Dumort., the potato and its wild relatives, contains about 200 wild species distributed from the southwestern United States to central Argentina and adjacent Chile (Hawkes, 1990; Spooner & Hijmans, 2001). Most species grow in the Andes, but the United States, Mexico, and Central America contain about 30 diploid taxa (2*n* = 24), as well as tetraploid (2*n* = 48) and hexaploid (2*n* = 72) ones. The United States, Mexico, and Central American diploids are classified in *Solanum* series *Bulbocastana*, *Morelliformia*, *Pinnatisecta*, *Polyadenia*, and *Tuberosa* (Hawkes, 1990); see Table 1 for authorities of series, species, and subspecies. For simplicity, we refer to species from this region as Mexican or primarily Mexican species. Some Mexican diploids appear very similar morphologically and led us to question whether they were valid species. In this paper we explore the use of morphology and microsatellites (or simple sequence repeats, SSRs) to test the validity of these primarily Mexican diploid species.

Hawkes (1989, 1990) divided *Solanum* sect. *Petota* into 21 series. Two of these series are non-tuber-bearing, and 19 are tuber-bearing. Hawkes (1989, 1990) placed the two non-tuber-bearing series in subsection *Estolonifera* Hawkes, and the remaining 19 tuber-bearing series in subsection *Potatoe* Don of *Solanum*. He divided subsection *Potatoe* into two superseries, *Stellata* Hawkes and *Rotata* Hawkes, based on the corolla shape. Hawkes (1990) and Hawkes and Jackson (1992) proposed a phylogeny of subsection *Potatoe* of *Solanum* based on data from morphology, biogeography, ploidy level, and Endosperm Balance Number. The Endosperm Balance Number (EBN) relates to a strong isolating mechanism in *Solanum* sect. *Petota* and explains success or failure of intra- and interspecific crosses, due to the functioning or breakdown of the endosperm after fertilization. The EBNs are hypothetical genetic factors independent of ploidy and empirically determined, relative to crossing with standard test EBN crossers of known EBN. In potato, these are 2x(1EBN), 2x(2EBN), 4x(2EBN), 4x(4EBN), and 6x(4EBN). Species can cross within EBN, irrespective of ploidy (Hanneman, 1994).

Hawkes (1990) and Hawkes and Jackson (1992) informally designated subsets of *Solanum* species within each superseries with more "primitive" or "advanced" morphological characters, providing four groups, primitive *Stellata*, advanced *Stellata*, primitive *Rotata*, and advanced *Rotata*. In this theory the Mexican diploids are primitive *Stellata* (in ser. *Bulbocastana*, *Morelliformia*, *Pinnatisecta*, and *Polyadenia*). All *Solanum* species in these series are 2x(1EBN). Representatives of these primitive *Stellata* in *Solanum* migrated to South America and remained primitive *Stellata* (ser. *Circaeifolia*, *Commersoniana*, *Lignicaulia*, *Olmosiana*). These then evolved to advanced *Stellata*, then to primitive *Rotata*, and finally to advanced *Rotata*. The species in Mexico that are advanced *Rotata* (*S. verrucosum* of ser. *Tuberosa*, and members of ser. *Conicibaccata*, *Demissa*, and *Longipedicellata*) either remigrated back from South America, or are products of hybridization between these remigrants and primitive indigenous Mexican diploids. For the sake of simplicity, all *Solanum* species of primitive *Stellata* in the United States, Mexico, and Guatemala will here be referred to as "primitive Mexican diploids."

Spooner et al. (1991) investigated the Hawkes (1990) *Stellata–Rotata* hypothesis using chloroplast DNA (cpDNA) restriction site analysis in *Solanum* series *Bulbocastana*, *Conicibaccata*, *Demissa*, *Longipedicellata*, *Morelliformia*, *Pinnatisecta*, *Polyadenia*, and *Tuberosa*. Their results gave partial support to the Hawkes (1989, 1990) and Hawkes and Jackson (1992) hypotheses, by supporting most primitive Mexican diploids as basal, and other Mexican species as advanced. Some putative primitive *Stellata* from South America, however, such as *Solanum circaeifolium* (ser. *Circaeifolia*), were later supported as derived by further cpDNA restriction site studies (Spooner & Sytsma, 1992; Spooner & Castillo, 1997).

Two other cpDNA restriction site studies investigated relationships of Mexican potatoes. Spooner and Sytsma (1992) produced a clado-

TABLE 1.

Location, series affiliation within *Solanum*, PI number, and collector, of the accessions examined in this study. Herbarium vouchers are deposited at PTIS, along with other known herbaria of deposition in the locality column (CIP = International Potato Center in Lima, Peru, INIFAP = the Mexican National Potato Program in Toluca, Mexico). [1]Accession number corresponds to Figs. 2, 4. [2]The map locality corresponds to Fig. 1. SA refers to South America and U refers to localities with unknown location beyond the country of origin. [3]United States Department of Agriculture Plant Introduction Numbers.

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
1	21	*Bulbocastana* (Rydb.) Hawkes	*Solanum bulbocastanum* Dunal subsp. *bulbocastanum*	275198	*Hawkes 1595*	MEXICO. **México**: Cerro de Cocotitlán (IBUG, MEXU, PTIS)
2	21		*S. bulbocastanum* subsp. *bulbocastanum*	275184	*Hawkes 1581*	MEXICO. **Federal District**: Pedregal de San Ángel, Ciudad Universitaria (IBUG, IEB, MEXU, PTIS, WIS)
3	23		*S. bulbocastanum* subsp. *bulbocastanum*	275194	*Hawkes 1591*	MEXICO. **Oaxaca**: ruins of Montealbán (IBUG, PTIS)
4	14		*S. bulbocastanum* subsp. *dolichophyllum* (Bitter) Hawkes	498224	*Ochoa 14162*	MEXICO. **Michoacán**: Las Palmitas (CIP, IBUG, K, PTIS, WIS)
5	21		*S. bulbocastanum* subsp. *dolichophyllum*	545752	*Tarn et al. 244*	MEXICO. **México**: E of Coatepéc Harinas, between San Francisco and Porfirio Díaz (B, K, IBUG, PTIS)
6	17		*S. bulbocastanum* subsp. *dolichophyllum*	255516	*Graham 300B*	MEXICO. **Jalisco**: Cuidad Guzmán (PTIS)
7	28		*S. bulbocastanum* subsp. *partitum* (Correll) Hawkes	558379	*Spooner et al. 4224*	MEXICO. **Chiapas**: 9.4 km S of Rt. 190 (from near Teopisca), to Las Rosas (IBUG, INIFAP, PTIS, WIS)
8	29		*S. bulbocastanum* subsp. *partitum*	275200	*Hawkes 1796*	GUATEMALA. **Huehuetenango**: rd. from Huehuetenango to Quezaltenango, 5 km S of Manlacatancito (C, K, PTIS)

TABLE 1 CONTINUED.

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
9	27		*S. clarum* Correll	558382	*Spooner et al. 4216*	MEXICO. **Chiapas**: 1.1 km N of town square of El Porvenir on rd. to Siltepecguez (IBUG, INIFAP, PTIS)
10	23	*Morelliformia* Hawkes	*S. morelliforme* Bitter & Münch	275220	*Hawkes 1648*	MEXICO. **Veracruz**: Km 305.5 from México on the rd. from Las Vigas to Jalapa, Malpaís de La Joya (C, K, P, PTIS)
11	16		*S. morelliforme*	275218	*Hawkes 1613*	MEXICO. **México**: 44.5 km from the main Toluca–Morelia Rd., towards Valle de Bravo from Toluca (C, PTIS, US)
12	16		*S. morelliforme*	498003	*Tarn et al. 48*	MEXICO. **México**: about 18.5 km towards Valle de Bravo from Toluca–Temascaltepec, Hwy. 134 via Rancho San Ramón (PTIS)
13	5	*Pinnatisecta* (Rydb.) Hawkes	*S. brachistotrichium* (Bitter) Rydb.	320265	*Hawkes 1234*	MEXICO. **Chihuahua**: Majalca, 40 mi. NW of Chihuahua, near the village (C, IBUG, PTIS, US)
14	5		*S. brachistotrichium*	498217	*Ochoa 14206*	MEXICO. **Chihuahua**: Rt. Chihuahua–Ciudad Juárez (CIP, IBUG, PTIS, US, WIS)
15	6		*S. brachistotrichium*	497993	*Tarn et al. 13*	MEXICO. **Chihuahua**: La Aurora at 41 km, along rd. to San Juanito from the La Junta to Yepachic Hwy. (PTIS)
16	8		*S. brachistotrichium*	545832	*Tarn et al. 207*	MEXICO. **Aguascalientes**: from Rincón de Ramos on Hwy. 45, 30 km along the track towards El Chiquihuitillo, Rancho Tierra Colorada (BR, C, K, MEXU, PTIS)

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
17	8		*S. brachistotrichium*	545815	*Tarn et al. 215*	MEXICO. **Aguascalientes**: Hwy. 70, about 33 km from Aguascalientes, 8.2 km along the track past Milpillas de Arriba towards Potrero (PTIS)
18	8		*S. brachistotrichium*	255527	*Graham 346 X 348*	MEXICO. **Aguascalientes**: between Aguascalientes and Calvillo (PTIS)
19	22		*S. cardiophyllum* Lindl. subsp. *cardiophyllum*	347759	*Tarn 241D*	MEXICO. **Puebla**: left side of Tehuacán–Huajuapan de León rd. on the Puebla side of border, Hwy. 125, almost at border of Puebla–Oaxaca states (PTIS)
20	U		*S. cardiophyllum* subsp. *cardiophyllum*	283062	*Graham s.n.*	MEXICO (PTIS)
21	U		*S. cardiophyllum* subsp. *cardiophyllum*	283063	*Graham s.n.*	MEXICO (PTIS)
22	11		*S. cardiophyllum* subsp. *ehrenbergii* Bitter	279272	*Hawkes 1458*	MEXICO. **Aguascalientes**: 7 mi. from Aguascalientes on the rd. to Loreto, 1.25 mi. from the main Aguascalientes to Zacatecas Hwy. (C, K, PTIS, US)
23	12		*S. cardiophyllum* subsp. *ehrenbergii*	184762	*Hawkes 1086*	MEXICO. **Querétaro**: San Juan del Río, SW of the town (ECON, PTIS)
24	8		*S. cardiophyllum* subsp. *ehrenbergii*	341231	*Commonwealth Potato Collection 2302*	MEXICO. **Jalisco**: Km 201 from Guadalajara on the rd. to San Luis Potosí (PTIS)
25	12		*S. cardiophyllum* subsp. *ehrenbergii*	186548	*Hawkes 1100*	MEXICO. **Zacatecas:** 726.5 km from México towards Zacatecas (LL, PTIS)
26	9		*S. cardiophyllum* subsp. *ehrenbergii*	255520	*Graham 371*	MEXICO. **San Luis Potosí** (PTIS)
27	12		*S. cardiophyllum* subsp. *ehrenbergii*	275213	*Hawkes 1428*	MEXICO. **Querétaro**: 3 km SSE of town (C, K, PTIS, US)

TABLE 1 CONTINUED.

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
28	22		*S. hintonii* Correll		*Spooner et al. 4033*	MEXICO. **México:** 6.5 km SW of Temascaltepec–Valle de Bravo rd., on rd. to San Pedro Tenayac, on S side of rd., ca. 50 m downstream of bridge over rd. (INIFAP, PTIS)
29	2		*S. jamesii* Torr.	458425	*Ugent & Ruhde 16-78*	U.S.A. **Arizona**: Apache Co., Hwy. 180, 3.2 km S of Eager at the junction with Rt. 130 (WIS, PTIS)
30	2		*S. jamesii*	564051	*Salas et al. 24*	U.S.A. **Arizona**: Apache Co., near Nelson reservoir, two mi. S on Rt. 666 then E 1 mi. on rd. 275 (PTIS)
31	3		*S. jamesii*	564049	*Salas et al. 21*	U.S.A. **New Mexico**: Catron Co., Reserve vicinity, at about 6 mi. NE of Aragon on Hwy. 12, at 33 mi. marker (from Hwy. 180) (PTIS)
32	1		*S. jamesii*	275169	*Hawkes 1176*	U.S.A. **New Mexico**: Grant Co., S end of the Big Burro Mountains, Silver City, 17 mi. from Lordsburg (Rt. 180) (K, PTIS)
33	1		*S. jamesii*	458423	*Ugent & Ruhde 7-78*	U.S.A. **New Mexico**: Grant Co., Hwy. 90, 43.5 km SW of Silver City, Gila National Forest (PTIS, WIS)
34	2		*S. jamesii*	275172	*Hawkes 1207*	U.S.A. **Arizona**: Cochise Co., Chiricahua Mountains, Monita Canon, just below Faraway Ranch at the edge of National Monument (K, PTIS)

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
35	20		*S.* ×*michoacanum* (Bitter) Rydb. (putative origin is *S. bulbocastanum* × *S. pinnatisectum*)	558497	*Spooner et al. 4077*	MEXICO. **Michoacán**: at km 21 marker along Rt. 120 S of Morelia, on W side of Rt. 120 (INIFAP, PTIS)
36	7		*S. nayaritense* (Bitter) Rydb.	545827	*Tarn et al. 270A*	MEXICO. **Nayarit**: near Sta. Anita, about 1.5 km NE of Sta. Teresa (PTIS)
37	8		*S. nayaritense*	545820	*Tarn et al. 234A*	MEXICO. **Zacatecas**: Hwy. 54, 10 km SW of Jalpa, 26.3 km along the track toward Tlaltenango (K, PTIS)
38	8		*S. nayaritense*	545825	*Tarn et al. 225*	MEXICO. **Zacatecas**: Hwy. 70, 12 km NW of Jalpa, 18 km along the track SE toward Tlachichila (K, PTIS)
39	13		*S. pinnatisectum* Dunal	275234	*Hawkes 1456*	MEXICO. **Jalisco**: 15 mi. from León on the rd. to Aguascalientes (C, IBUG, K, MEXU, PTIS, US)
40	11		*S. pinnatisectum*	184764	*Hawkes 1093*	MEXICO. **Guanajuato**: León, 2 km SE of the cement factory (BR, IBUG, K, LL, MEXU, MPU, NY, PTIS, WAG)
41	14		*S. pinnatisectum*	275233	*Hawkes 1455*	MEXICO. **Guanajuato**: 2 mi. from Siláo on the rd. to Guanajuato, El Castillo (C, IBUG, K, MEXU, PTIS)
42	13		*S. pinnatisectum*	275236	*Hawkes 1505*	MEXICO. **Jalisco**: 29 mi. from Guadalajara on the rd. to Mexico City, hacienda de Huejotitan (C, IBUG, K, MEXU, PTIS, US)
43	12		*S. pinnatisectum*	275230	*Hawkes 1424*	MEXICO. **Querétaro**: 3 km SSE of town, by the small reservoir (IBUG, K, MEXU, PTIS)
44	20		*S. pinnatisectum*	190115	*Baldwin 14374*	MEXICO. **Michoacán**: Morelia (LL, NA, PTIS)
45	13		*S. bulbocastanum* × *S. cardiophyllum* putative hybrid		*Rodríguez 2592*	MEXICO. **Jalisco**: Sierra de La Primavera (PTIS)

TABLE 1 CONTINUED.

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
46	11		*S.* ×*sambucinum* Rydb. (putative origin is *S. ehrenbergii* × *S. pinnatisectum*)	595478	*Rodríguez 2563*	MEXICO. **Querétaro**: foot-hills of "El Buey" mountain, on junction of roads of Querétaro–San Luis Potosí and Mexico City–San Luis Potosí (F, IBUG, MICH, MO, NY, PTIS)
47	18		*S.* ×*sambucinum*	604209	*Rodríguez 2565*	MEXICO. **Guanajuato**: La Purísima, municipality of San Diego de la Unión, rd. from Querétaro city to San Luis Potosí (MICH, PTIS)
48	10		*S. stenophyllidium* Bitter	558460	*Spooner et al. 4104*	MEXICO. **Jalisco**: rd. from N side of Guadalajara, past side rd. to San Francisco Tesistán to San Cristóbal de la Barranca, on W side of rd., 20.5 km (by posted km signs), N of Guadalajara, about 0.5 km S of Mirador (INIFAP, PTIS)
49	16		*S. tarnii* Hawkes & Hjert.	498048	*Tarn et al. 79*	MEXICO. **Hidalgo**: from Las Trancas, Hwy. 85, Zimapan to Jacala (K, PTIS)
50	16		*S. tarnii*	545808	*Tarn et al. 257*	MEXICO. **Hidalgo**: turning off Hwy. 85 (Zimapan/Jacala) at Las Trancas, go 6.4 km along rd. towards Nicolás Flores (C, F, K, MEXU, PTIS, WAG)
51	15		*S. tarnii*	545742	*Tarn et al. 56*	MEXICO. **Veracruz**: about 14 km S of Huayacocotla, near Viborillos, on rd. to Tulancingo (K, PTIS)
52	16		*S. tarnii*	498043	*Tarn et al. 57*	MEXICO. **Hidalgo**: 28 km S of Huayacocotla, 8 km before Agua Blanca (C, K, MEXU, PTIS)

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
53	16		*S. tarnii*	570641	*Hjerting 7361*	MEXICO. **Hidalgo**: 20 km from Agua Blanca towards Huayacocotla, near Palo Bendito (PTIS)
54	17		*S. trifidum* Correll	255542	*Canada Ottawa 460*	MEXICO. **Michoacán**: Km 48 on the Carapan–Uruapan Hwy. (PTIS)
55	18		*S. trifidum*	558478	*Spooner et al. 4283*	MEXICO. **Michoacán**: on rd. from Rt. 120 NW to Cheran, 2.5 km SE of Serina (INIFAP, PTIS, WIS)
56	17		*S. trifidum*	558480	*Spooner et al. 4089B*	MEXICO. **Michoacán**: along microwave tower rd. off of dirt rd. beginning about 5 km NE of Capacuaro, 5.9 km from beginning of this microwave tower rd. (INIFAP, PTIS)
57	17		*S. trifidum*	283104	*Hawkes 1541*	MEXICO. **Jalisco**: NE slope of Nevado de Colima, 13 km from turn to Tolimán on the rd. from Ciudad Guzmán, Los Alpes (IBUG, K, MEXU, PTIS)
58	U		*S. trifidum*	292213	*Ugent 5745*	MEXICO (PTIS)
59	26	*Polyadenia* Bukasov	*S. lesteri* Hawkes & Hjert.	558434	*Spooner et al. 4155*	MEXICO. **Oaxaca**: on W side of Rt. 125, 3.4 km S of Rt. 190, just S of San Juan Teposcolula (INIFAP, PTIS, WIS)
60	26		*S. lesteri*	442694	*Hawkes et al. 1714*	MEXICO. **Oaxaca**: 25.8 km S of Miahuatlán on the Oaxaca–Puerto Ángel rd. (K, PTIS)
61	26		*S. lesteri*	558435	*Spooner et al. 4177*	MEXICO. **Oaxaca**: along E side of Rt. 175, at km 134.1, about 50 m off rd.; up a slope, S of Miahuatlán de Porfirio Díaz (INIFAP, PTIS, WIS)

TABLE 1 CONTINUED.

Accession Number[1]	Map Locality[2]	Series placement by Hawkes (1990)	Taxon	PI[3]	Collector	Locality
62	22		*S. polyadenium* Greenm.	498036	*Tarn et al. 65*	MEXICO. **Hidalgo**: Hwy. 85, Zimapan to Tamzunchale, at Las Trancas, about 8 km E at Jaguey on the track to Nicolás Flores (PTIS)
63	13		*S. polyadenium*	558450	*Spooner et al. 4137*	MEXICO. **Jalisco**: on microwave tower rd. to Cerro Grande, SE of Sante Fé, 1.1 km downhill of top of town (INIFAP, PTIS, WIS)
64	24		*S. polyadenium*	161728	*Correll 14374*	MEXICO. **Michoacán**: near Matugeo (ECON, GAT, MEXU, PTIS)
65	25		*S. polyadenium*	347769	*Tarn & Gómez 221*	MEXICO. **Puebla**: New México–Veracruz, toll rd., at km 208.5 (K, PTIS)
66	19		*S. polyadenium*	347770	*Tarn & Gómez 234*	MEXICO. **Veracruz**: near Puerto del Aire, on old Orizaba–México rd., Rt. 150, between Puerto and Veracruz–Puebla state boundary (K, PTIS)
67	SA	*Circaeifolia* Hawkes	*S. circaeifolium* Bitter	498188	*Hawkes et al. 6581*	BOLIVIA. **Cochabamba**: Ayopaya, near Independencia, Ichupampa (PTIS)
68	SA	*Commersonia* Bukasov	*S. commersoni* Dunal	566751	*Hoffman s.n.*	ARGENTINA (PTIS)
69	SA	*Conicibaccata* Bitter	*S. santollalae* Vargas	473372	*Hawkes et al. 5103*	PERU. **Cuzco**: Paucartambo, Pillahuata (PTIS)
70	SA	*Lignicaulia* Hawkes	*S. lignicaule* Vargas	275273	*E. Baur Sortiment 1884*	PERU. **Cuzco**: Calca, Pisac (PTIS)
71	2	*Longipedicellata* Bukasov	*S. fendleri* subsp. *fendleri* Hawkes	275163	*Hawkes 1180*	U.S.A. **Arizona**: Cochise Co., Chiricahua Mountains, Rustler Park (K, PTIS)
72	16	*Tuberosa* (Rydb.) Hawkes	*S. verrucosum* Schltdl.	275260	*Hawkes 1658*	MEXICO. **Hidalgo** (AA, BM, C, K, PTIS)

gram that divided the primitive Mexican diploid species into these clades in *Solanum*: (1) series *Pinnatisecta*, with internested series *Polyadenia*, *Bulbocastana* (in part), and series *Morelliformia*; (2) *S. bulbocastanum* and *S. cardiophyllum*; and (3) *S. verrucosum* and all Mexican polyploid species. The second clade was unexpected because all prior hypotheses suggested that *S. bulbocastanum* and *S. cardiophyllum* would associate with the first clade. *Solanum verrucosum*, on the other hand, was long recognized by morphological and crossing data to truly be distinct and to belong in the third clade. Rodríguez and Spooner (1997) reanalyzed the *Solanum bulbocastanum* and *S. cardiophyllum* clade including more accessions and all the subspecies of each species. The resulting tree maintained all the subspecies in the same clade except for all the accessions of *S. cardiophyllum* subsp. *ehrenbergii*. This subspecies was placed in the basal Mexican diploid clade, most closely related to *S. brachistotrichium* and *S. stenophyllidium*.

The basal relationship of the primitive *Stellata* within *Solanum* sect. *Petota,* including *S. circaeifolium* of series *Circaeifolia,* was further investigated by Kardolus (1998) using amplified fragment length polymorphisms (AFLP). *Solanum circaeifolium* was shown to be primitive by AFLPs and nested with the Mexican diploids, unlike cpDNA results (Spooner & Castillo, 1997), suggesting a "chloroplast capture" event, known to be common throughout angiosperms (Rieseberg & Brunsfeld, 1992). Its primitive position, however, matched the *Stellata/Rotata* hypothesis of Hawkes (1989, 1990) and Hawkes and Jackson (1992).

Microsatellites are hypervariable molecular markers (Tautz, 1989; Powell et al., 1996), consisting of tandem repeats of 1 to 6 bp (Provan et al., 1996b; Rubinsztein et al., 1999; Bichara et al., 2000). They have been used in cultivar identification (Smulders et al., 1997; Lin & Walker, 1998), germplasm analysis (Powell et al., 1996), the development of quantitative trait loci (QTL) (Arens et al., 1995; Areshchenkova & Ganal, 1999; Winter et al., 1999; Lorieux et al., 2000), to detect genetic polymorphisms (Russell et al., 1997; Nader et al., 1999; Teulat et al., 2000), and in phylogenetic studies (Kostia et al., 2000; Petren et al., 1999; Clisson et al., 2000; Raker & Spooner, 2002). In potato they have been used mainly for cultivar identification (Milbourne et al., 1997; Schneider & Douches, 1997), to develop linkage groups (Milbourne et al., 1998), in germplasm identification (Provan et al., 1996b), in analysis of intra-specific somatic hybrids (Provan et al., 1996a), and in genetic analysis of anther-derived haploid potatoes (Veilleux et al., 1995).

Milbourne et al. (1998) developed microsatellite primers and mapped them to all 12 linkage groups of cultivated potato, *S. tuberosum*. We wished to test their use to investigate the validity and interspecific relationships of the primitive Mexican diploids and other primitive and advanced potatoes, including members of Hawkes's (1990) primitive *Stellata*. Raker and Spooner (2002) showed these primers to be of use to distinguish the subspecies of *S. tuberosum*, but this was the very germplasm base from which these primers were developed. We needed these data for our ongoing floristic studies of *Solanum* sect. *Petota* in North America, Mexico, and Central America. This included investigations of hybrid origins for some of these species. These hybrids and putative origins by Hawkes (1990) are *S.* ×*michoacanum* (*S. bulbocastanum* × *S. pinnatisectum*), and *S.* ×*sambucinum* (*S. cardiophyllum* subsp. *ehrenbergii* × *S. pinnatisectum*). In addition, Rodríguez and Vargas-P. (1994) postulated a new unnamed hybrid of *S. bulbocastanum* × *S. cardiophyllum* (no subspecies designated for either species). We include South American primitive *Stellata* species to test the Hawkes (1989, 1990) and Jackson and Hawkes (1992) hypotheses of relationships in *Solanum*.

MATERIALS AND METHODS

PLANT MATERIAL

More than one accession per taxon was analyzed (when available) from as many geographically dispersed sites as possible (Table 1, Fig. 1). The plants were grown in the greenhouse, because many of the primitive Mexican diploids do not thrive outdoors in Wisconsin. An average of three plants per accession of the Mexican diploids were grown, and one accession per series from the South American diploids. *Solanum stenophyllidium* had only one accession available as seeds, and we analyzed two separate sets of three plants per the same accession for morphological analysis.

MORPHOLOGY AND DATA ANALYSIS

Morphological characters were measured when the plants were in full flower (Table 2). Significant differences in character states for quantitative characters were studied by the Tukey-Kramer test, and qualitative characters by the Likelihood Ratio Chi square test and Pearson Chi square test in JMP statistical software v. 3.1.5 (SAS Institute Inc., 1998). Phenetic analyses were performed with NTSYS-pc (Rohlf, 1992). An operational taxonomic unit (OTU) was the average of three individuals per accession. Data were standardized (STAND), and similarity matrices (in SIMINT), average taxonomic distance (DIST), Euclidean distance (EUCLID), Manhattan distance (MANHAT), and product-moment correlation (CORR) were generated. Clustering was performed with the unweighted pair-group method, UPGMA (Sokal & Sneath, 1963), and Neighbor Joining, NJ (Saitou & Nei, 1987). Cophenetic correlation coefficients (COPH, in MXCOMP) were used to measure the distortion between similarity matrices and the resultant four phenograms. Stepwise discriminate analyses (SDA) were performed by SAS v.7 (SAS Institute Inc., 1998) using Stepwise discriminate analysis (STEPDISC).

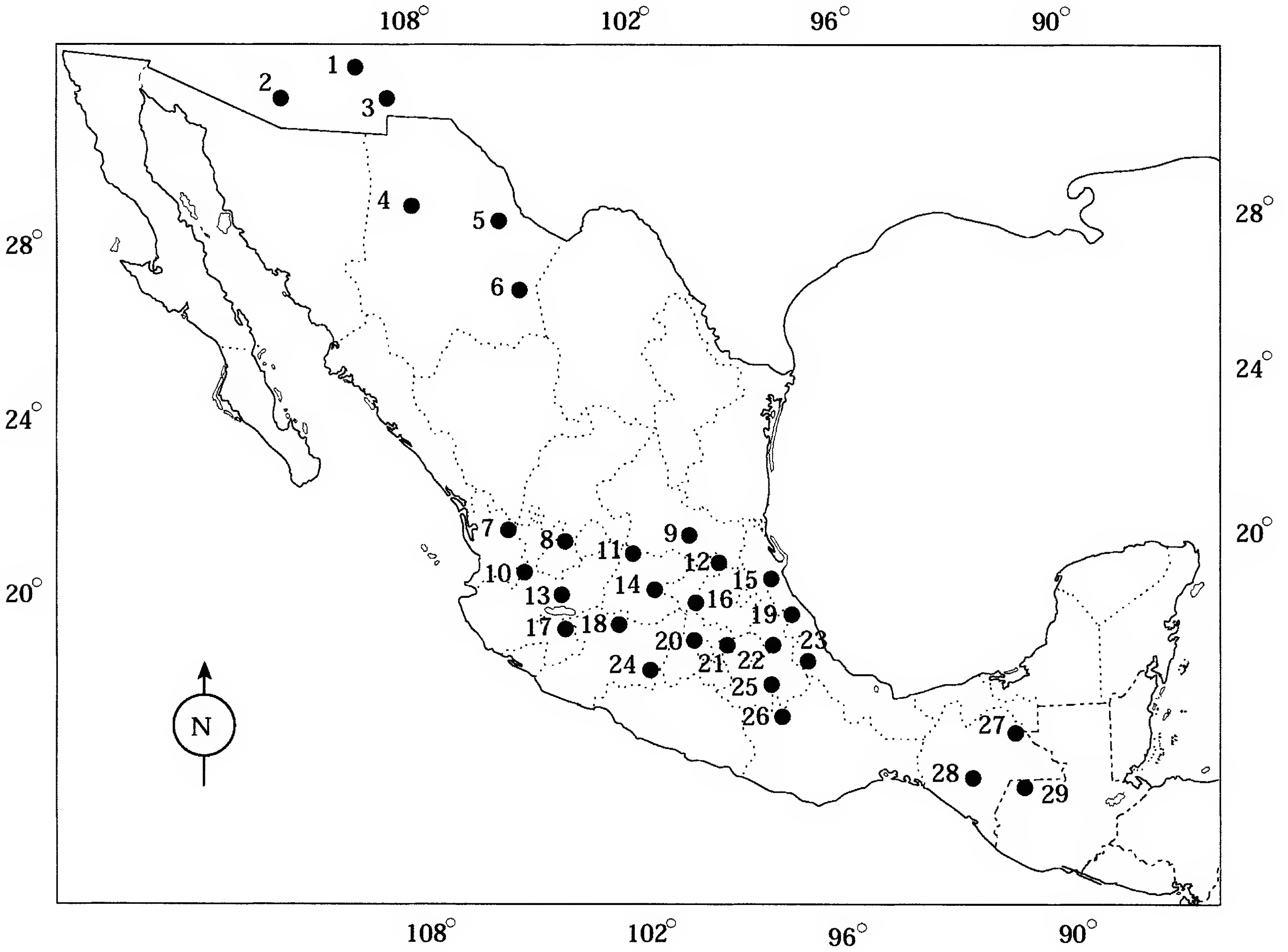

Figure 1. Distribution of wild potato accessions used in this study from the United States, Mexico, and Guatemala. Accessions from South America are not mapped. Numbers correspond to generalized map localities in Table 1.

TABLE 2.

Morphological characters measured. All values are in cm, unless otherwise indicated. The 35 of 56 statistically significant characters (*P* = 0.05, SAS Institute Inc., 1998) distinguishing all taxa (see text) are marked with an asterisk (*).

STEM CHARACTERS

1. Stem pubescence length (mm)*. 2. Stem pubescence posture: pointing up (1), pointing down (2), pointing out (3)*. 3. Stem diameter (mm)*. 4. Stem wings: present (1), absent (2). 5. Stem shape: angular (1), rounded (2)*. 6. Pubescence type: glabrescent (1), pubescent (2)*.

LEAF CHARACTERS

7. Leaf width*. 8. Ratio: leaf length/width*. 9. Number of leaflet pairs. 10. Leaflet position: alternate (1), opposite (2). 11. Widest leaflet pair: terminal (1), most distal lateral leaflet pair (2), second most distal lateral leaflet pair (3)*. 12. Interstitial leaflets: present (1), absent (2)*. 13. Terminal leaflet width*. 14. Ratio: length/width of terminal leaflet blade*. 15. Length from widest point of terminal leaflet blade to base of blade*. 16. Ratio: length from widest point of terminal leaflet blade to base of blade/length of terminal leaflet blade. 17. Petiolule length of terminal leaflet*. 18. Most distal lateral leaflet width*. 19. Ratio: length of most distal lateral leaflet blade/width of most distal lateral leaflet*. 20. Length from widest point of most distal lateral leaflet blade to base of blade*. 21. Ratio: length from widest point of most distal lateral leaflet blade to base of blade/length of most distal lateral leaflet blade*. 22. Petiolule length of most distal lateral leaflet*. 23. Second most distal lateral leaflet width*. 24. Ratio: length of second most distal lateral leaflet blade/width of second most distal lateral leaflet*. 25. Length from widest point of second most distal lateral leaflet blade to base of blade*. 26. Ratio: length from widest point of second most distal lateral leaflet blade to base of blade/length of second most distal lateral leaflet blade. 27. Petiolule length of second most distal lateral leaflet*. 28. Abaxial leaf pubescence length (mm)*. 29. Abaxial leaf pubescence posture: pointing up (1), pointing down (2), pointing out (3). 30. Lateral leaflet decurrency: decurrent (1), not decurrent (2)*. 31. Petiole wings: present (1), absent (2)*. 32. Petiole length*. 33. Shape of pseudostipular leaflet: pinnulate (1), lunate (2)*. 34. Spicy odor: present (1), absent (2)*.

FLORAL CHARACTERS (see Spooner & van den Berg, 1992, for illustrations of characters 49–52).

35. Peduncle length. 36. Length from the base to the articulation of the pedicel*. 37. Ratio: pedicel length/length from base to the articulation of the pedicel. 38. Length of calyx (mm). 39. Ratio: length of calyx lobe/length of calyx*. 40. Posture of calyx lobe: straight (1), bent over (2), curled around (3). 41. Symmetry of calyx: symmetrical (1), asymmetrical (2). 42. Length of calyx acumen (mm)*. 43. Ratio: length of calyx lobe/length of calyx acumen (mm). 44. Calyx color: green (1), purple (2), green and purple (3). 45. Position of calyx and corolla: alternate (1), opposite (2). 46. Style exsertion (mm). 47. Length of anther (mm). 48. Length of anther filament (mm). 49. Radius of the corolla measured from the center of the corolla to the tip of the corolla lobes (mm). 50. Ratio: Radius of the corolla measured from the center of the corolla to the tip of the corolla lobes/distance between the center of the flower and the junction of the corolla lobes (mm)*. 51. Width of the corolla lobe measured at the base of the corolla junction (mm)*. 52. Ratio: width of the corolla lobe measured at the base of the corolla junction/length from a line drawn across widest point of corolla lobes (mm). 53. Primary color of the abaxial surface of the corolla: white (1), creamy white (2), purple (3)*. 54. Secondary color of the abaxial surface of the corolla: white (1), creamy white (2), purple (3). 55. Posture of style: erect (1), curved (2).

FRUIT CHARACTERS

56. Fruit shape: globose (1), conical (2)*.

We used stepwise discriminant analysis to discover characters that best distinguished the nine most phenetically similar primitive Mexican diploid species (*Solanum brachistotrichum*, *S. cardiophyllum* subsp. *ehrenbergii*, *S. hintonii*, *S. jamesii*, *S.* ×*michoacanum*, *S. nayaritense*, *S. stenophyllidium*, *S. trifidum*, *S. tarnii*), with all procedures as above.

DNA EXTRACTION, AMPLIFICATION, AND DNA FRAGMENT ANALYSIS

DNA was extracted using the protocol in Raker and Spooner (2002). Forty-five mapped primers were selected from Milbourne et al. (1998) that were designed for *S. tuberosum* and screened for ability to amplify a fragment in these species: stm0001, stm0003, stm0007, stm0010, stm0013, stm0014, stm0017, stm0019, stm0024, stm0025, stm0028, stm0032, stm0037, stm0038, stm0051, stm0052, stm1003, stm1005, stm1008, stm1017, stm1020, stm1021, stm1024, stm1025, stm1029, stm1031, stm1041, stm1049, stm1055, stm1058, stm1064, stm1069, stm1100, stm1102, stm1104, stm1106, stm2005, stm2012, stm2013, stm2020, stm2022, stm2028, stm3009, stm3010, stm3016. Forward primers were labeled with fluorescent dyes FAM (blue), HEX (yellow), and TETRA (green), from PE Biosystems, to amplify individual accessions of all of the species. Reaction conditions were optimized, modifying conditions listed in Provan et al. (1996b). Conditions for a 25 µl reaction included 1X PCR Buffer II (Perkin Elmer), 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.4 µM of each primer pair, 1 unit of AmpliTaq Gold® (Perkin Elmer), and 10–20 ng of DNA. The annealing temperature followed Milbourne et al. (1998) or 1°C to 2°C below (Table 3). All reactions were amplified in a 9600 PE thermocycler with the following times and temperatures: 1 cycle for 10 min. at 94°C, 2 min. to anneal temperature, 5 min. at 72°C, 29 cycles of 1 min. at 94°C, 45 sec. to anneal, 5 min. at 72°C, ending with a 72°C hold for 45 min.

The microsatellite products for each individual were pooled in dye combinations of 3 µl FAM: 6 µl TETRA: 9 µl HEX, or in some cases each product was analyzed separately. PCR products were sent to the Biotechnology Center at the University of Wisconsin-Madison for fragment separation. Products were processed as follows: 1.5 µl aliquots of PCR product were mixed with 1.8 µl sample loading buffer (80% formamide, 10 mg/ml dextran blue, 5 mM EDTA at pH 8.0) and 0.45 µl of TAMRA 500 molecular weight standard (PE Biosystems). The mixture was heated for 3 min. at 95°C and then placed on ice. Approximately 1 µl of the cold samples was loaded on a 5% LongRanger™ (FMC Bioproducts) polyacrylamide/6M urea gel in a PE Biosystems 377XL DNA sequencing machine. Samples were run at 3000 V with 2400 scans/hour in 36 cm well-to-read plates. Data were collected using a PE Biosystems DNA Sequencer data collection v. 2.0 and analyzed with GeneScan v. 2.1 (PE Biosystems). Data were later imported in to Genotyper v. 2.1 PE Applied Biosystems for allele sizing, both automatically and manually. Peaks were scored as allele sizes in bp and manually translated into binary presence/absence.

MICROSATELLITE DATA ANALYSIS

The multistate matrix was imported to Microsat v. 1.5d (Minch et al., 1997) to produce distance matrices with two models, absolute difference and delta mu squared $(\partial\mu)^2$, both of which assume a step-wise mutation model (SMM) (Goldstein et al., 1995). New mutations following this model are obtained by adding or subtracting repeats one by one (Goldstein et al., 1995). These distance matrices were later imported into PAUP 4.0b3a (Swofford, 1998) to build trees with UPGMA (Sokal & Sneath, 1963) and NJ (Saitou & Nei, 1987).

The binary matrix was imported into PAUP 4.0b3a (Swofford, 1998) to produce the distance matrix of Nei and Li (1979) that applies the infinite allele model (IAM), where every mutation produces a new allele of potentially infinite size (Kimura & Crow, 1964). The Nei and Li matrix was used to build UPGMA (Sokal & Sneath, 1963) and NJ (Saitou & Nei, 1987) trees.

TABLE 3

Primer pairs used in the present study. Tag codes refer to fluorescent dyes: B = blue (FAM), G = green (TETRA), Y = yellow (HEX). Primer sequences, target repeat, and linkage group from *Solanum tuberosum* from Milbourne et al. (1998).

Primer	Tag	Primer sequence	Targeted repeat	Size range (bp)	Annealing	Chromosome Temp. (°C)	Percent missing data
stm0003-f	B	gga gaa tca taa caa cca g	(ac)9 (at)9	101–170	48	XII	4%
stm0003-r		aat tgt aac tct gtg tgt gtg					
stm0007-f	B	gga caa gct gtg aag ttt at	(ac)9	185–234	52	XII	58%
stm0007-r		aat tga gaa aga gtg tgt gtg					
stm0014-f	G	cag tct tca gcc cat agg	(gt)5 (at)7 (gt)10	77–201	53	I	18%
stm0014-r		taa aca atg gta gac aag aca aa					
stm0051-f	Y	tac ata cat aca cac acg cg	(ac)7…(ac)7 (at)4	84–116	53	X	23%
stm0051-r		ctg caa ctt ata gcc tcc a					
stm1005-f	B	atg cct ctt acg aat aac tcg g	(gta)6	160–187	59	VIII	27%
stm1005-r		cag cta acg tgg ttg ggg					
stm1017-f	G	gac acg ttc acc ata aa	(att)5	115–137	48	IX	21%
stm1017-r		aga aga ata gca aag caa					
stm1024-f	B	ata cag gac ctt aat ttc ccc aa	(ttg)6	125–152	59	VIII	13%
stm1024-r		tca aaa ccc aat tca atc aaa tc					
stm1029-f	Y	agg ttc act cac aat caa agc a	(c)12	121–166	58	I	41%
stm1029-r		aag att tcc aag aaa ttt gag gg					
stm1041-f	B	gtt gag tag aag gag gat t	(gaa)5	86–101	53	V	13%
stm1041-r		cct ttg tct tct gct ttt g					
stm1049-f	G	cta cca gtt tgt tga ttg tgg tg	(ata)6	176–212	58	I	27%
stm1049-r		agg gac ttt aat ttg ttg gac g					
stm2022-f	B	gcg tca gcg att tca gta cta	(caa)3…(caa)3	167–266	57	II	16%
stm2022-r		ttc agt caa ctc ctg ttg cg					
stm3009-f	B	tca gct gaa cga cca ctg ttc	(tc)13	131–211	63	VII	4%
stm3009-r		gat ttc acc aag cat gga agt c					

RESULTS

MORPHOLOGY

Thirty-five of the 56 characters were significantly different among all taxa (Table 2) as determined by the Tukey-Kramer test and the Likelihood Ratio Chi square test and Pearson Chi square test for qualitative characters in JMP v. 3.1.5 (SAS Institute Inc., 1998) statistical software. The cophenetic correlation coefficient determined that the UPGMA tree constructed with EUCLID had the highest (best) value of r = 0.835, followed by DIST (r = 0.827), MANHAT (r = 0.812), and CORR (r = 0.747). These four similarity matrices with NJ always provided lower r scores. The resulting UPGMA dendrogram (Fig. 2) supported most of the species. We will concentrate discussion of the primitive Mexican diploid species because this morphological study was designed mainly to search for phenetic support of these. Figure 2 is labeled as clusters A–I for ease of discussion.

Cluster A is well defined and includes all species and subspecies in *Solanum* ser. *Bulbocastana* (*Solanum bulbocastanum* subsp. *bulbocastanum*, subsp. *dolichophyllum*, subsp. *partitum*, and *S. clarum*). Both of these species perfectly support Hawkes's (1990) concept of this series. However, *Solanum bulbocastanum* subsp. *dolichophyllum* is intermixed with subspecies *partitum*. Cluster B includes both species in Hawkes's series *Polyadenia* (*S. lesteri*, *S. polyadenium*), likewise providing support for this series.

Clusters C–I include all members of Hawkes's (1990) series *Pinnatisecta*, plus other 2x(1EBN) species from South America in series *Circaeifolia*, *Commersoniana*, *Lignicaulia*, and *S. santolallae* (2x[2EBN], ser. *Conicibaccata*). Cluster C includes *S. cardiophyllum* subsp. *cardiophyllum* and *S.* ×*sambucinum* (both *Solanum* ser. *Pinnatisecta*) and *S. circaeifolium* (ser. *Circaeifolia*). *Solanum* ×*sambucinum* was of putative origin with none of these but with *S. pinnatisectum* and *S. cardiophyllum* subsp. *ehrenbergii* and *S. pinnatisectum*. Cluster D includes *S. pinnatisectum* and *S. lignicaule* (ser. *Lignicaulia*). Cluster E includes species-specific subclusters *S. tarnii* and *S. trifidum* that group together, the putative hybrid *S.* ×*michoacanum* (*S. bulbocastanum* × *S. pinnatisectum*), one "misplaced" or misidentified accession of *S. brachistotrichium*, the sole accession of *S. hintonii* (ser. *Pinnatisecta*), and *S. commersonii* (ser. *Commersoniana*). Cluster F includes both accessions of *S. nayaritense* (ser. *Pinnatisecta*) and the putative hybrid *S. bulbocastanum* × *S. cardiophyllum* (containing members of both ser. *Bulbocastana* and *Pinnatisecta*; Rodríguez et al., 1995). Cluster G contains all accessions of *S. jamesii* (ser. *Pinnatisecta*), and cluster H all accessions of *S. cardiophyllum* subsp. *ehrenbergii* plus one accession of *S. brachistotrichium* (ser. *Pinnatisecta*). Cluster I contains four of the six accessions of *S. brachistotrichium* and both replicate groups of the sole accession of *S. stenophyllidium* (ser. *Pinnatisecta*), but they do not group adjacent to each other.

In summary, the primitive Mexican diploid species are well supported phenetically except for *S. brachistotrichium*. *Solanum stenophyllidium* is problematic, perhaps due to a single accession examined, but groups with most accessions of *S. brachistotrichium*. The putative hybrid *S.* ×*sambucinum* groups between its parents, and the putative hybrids *S.* ×*michoacanum* and *S. bulbocastanum* × *S. cardiophyllum* away from their parents. The principal component analysis (not shown) presents a very similar clustering, or lack of it, regarding *S. brachistotrichium*.

Stepwise discriminant analysis separated all taxa by the following 21 morphological characters (cf. see Fig. 3), arranged from highest to lowest discriminant ability: (1) lateral leaflet decurrency (character 30, Table 2); (2) stem pubescence type (6); (3) spicy odor of leaves (34); (4) presence of interstitial leaflets (12); (5) ratio: length from widest point of most distal lateral leaflet blade to base of blade/length of most distal lateral leaflet blade (21); (6) shape of pseudostipular leaflet (33); (7) abaxial leaf pubescence length (28); (8) ratio: length of second most distal lateral leaflet blade/width of second most distal lateral leaflet (24); (9) presence of stem wings (4); (10) petiolule length of most distal lateral leaflet (22); (11) widest leaflet pair (11); (12) ratio: length of most

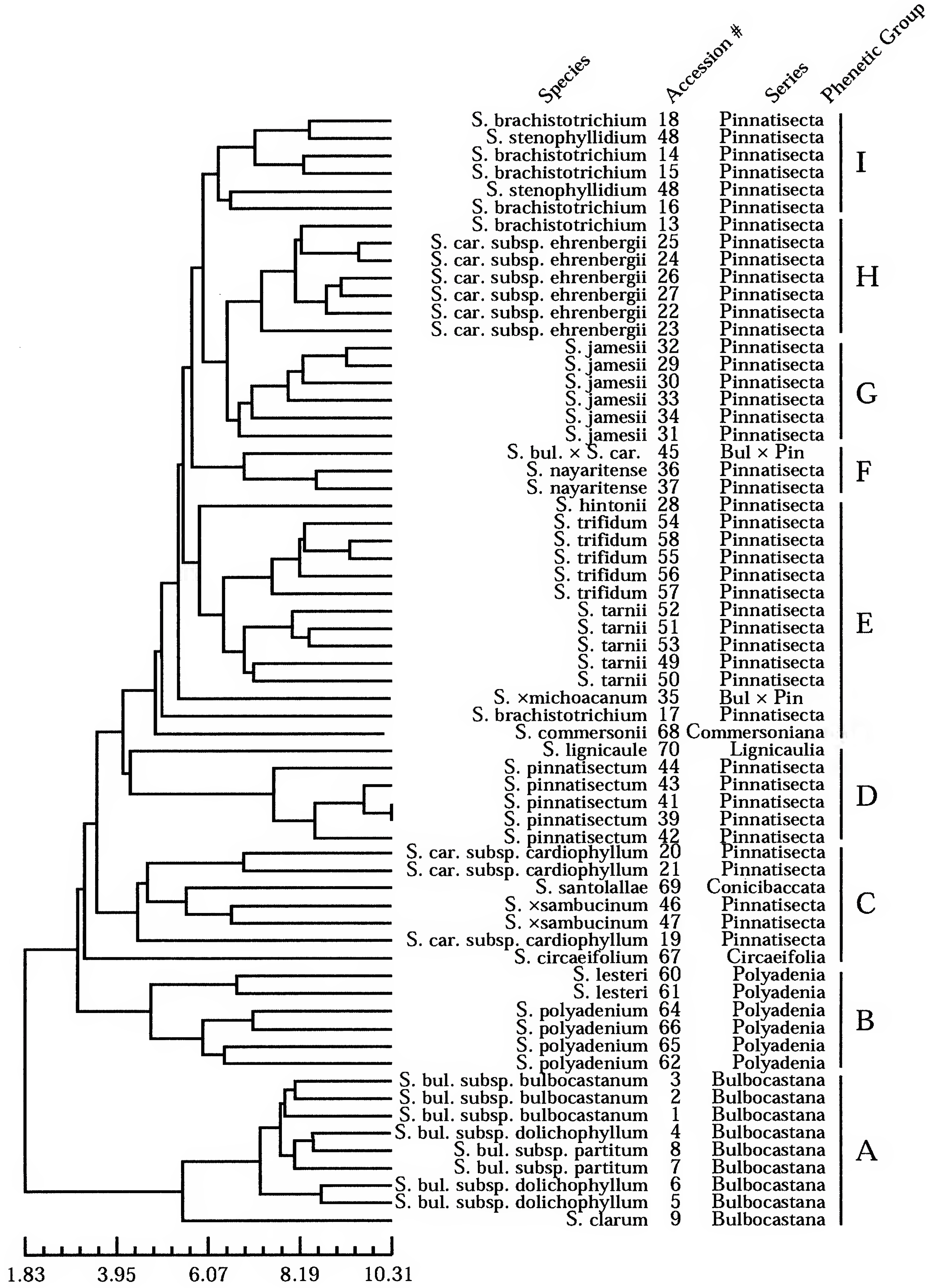
Species
Accession #
Series
Phenetic Group
S. brachistotrichium 18 Pinnatisecta
S. stenophyllidium 48 Pinnatisecta
S. brachistotrichium 14 Pinnatisecta
S. brachistotrichium 15 Pinnatisecta
S. stenophyllidium 48 Pinnatisecta
S. brachistotrichium 16 Pinnatisecta
I
S. brachistotrichium 13 Pinnatisecta
S. car. subsp. ehrenbergii 25 Pinnatisecta
S. car. subsp. ehrenbergii 24 Pinnatisecta
S. car. subsp. ehrenbergii 26 Pinnatisecta
S. car. subsp. ehrenbergii 27 Pinnatisecta
S. car. subsp. ehrenbergii 22 Pinnatisecta
S. car. subsp. ehrenbergii 23 Pinnatisecta
H
S. jamesii 32 Pinnatisecta
S. jamesii 29 Pinnatisecta
S. jamesii 30 Pinnatisecta
S. jamesii 33 Pinnatisecta
S. jamesii 34 Pinnatisecta
S. jamesii 31 Pinnatisecta
G
S. bul. × S. car. 45 Bul × Pin
S. nayaritense 36 Pinnatisecta
S. nayaritense 37 Pinnatisecta
F
S. hintonii 28 Pinnatisecta
S. trifidum 54 Pinnatisecta
S. trifidum 58 Pinnatisecta
S. trifidum 55 Pinnatisecta
S. trifidum 56 Pinnatisecta
S. trifidum 57 Pinnatisecta
S. tarnii 52 Pinnatisecta
S. tarnii 51 Pinnatisecta
S. tarnii 53 Pinnatisecta
S. tarnii 49 Pinnatisecta
S. tarnii 50 Pinnatisecta
S. ×michoacanum 35 Bul × Pin
S. brachistotrichium 17 Pinnatisecta
E
S. commersonii 68 Commersoniana
S. lignicaule 70 Lignicaulia
S. pinnatisectum 44 Pinnatisecta
S. pinnatisectum 43 Pinnatisecta
S. pinnatisectum 41 Pinnatisecta
S. pinnatisectum 39 Pinnatisecta
S. pinnatisectum 42 Pinnatisecta
D
S. car. subsp. cardiophyllum 20 Pinnatisecta
S. car. subsp. cardiophyllum 21 Pinnatisecta
S. santolallae 69 Conicibaccata
S. ×sambucinum 46 Pinnatisecta
S. ×sambucinum 47 Pinnatisecta
S. car. subsp. cardiophyllum 19 Pinnatisecta
S. circaeifolium 67 Circaeifolia
C
S. lesteri 60 Polyadenia
S. lesteri 61 Polyadenia
S. polyadenium 64 Polyadenia
S. polyadenium 66 Polyadenia
S. polyadenium 65 Polyadenia
S. polyadenium 62 Polyadenia
B
S. bul. subsp. bulbocastanum 3 Bulbocastana
S. bul. subsp. bulbocastanum 2 Bulbocastana
S. bul. subsp. bulbocastanum 1 Bulbocastana
S. bul. subsp. dolichophyllum 4 Bulbocastana
S. bul. subsp. partitum 8 Bulbocastana
S. bul. subsp. partitum 7 Bulbocastana
S. bul. subsp. dolichophyllum 6 Bulbocastana
S. bul. subsp. dolichophyllum 5 Bulbocastana
S. clarum 9 Bulbocastana
A
1.83
3.95
6.07
8.19
10.31

Figure 2. UPGMA dendrogram (Euclidean similarity option) based on 35 of 56 morphological characters that differ significantly among taxa. Species names and accession numbers, as in Table 1 and Figures 1 and 4, and phenetic groups as discussed in the text.

distal lateral leaflet blade/width of most distal lateral leaflet (19); (13) terminal leaflet width (13); (14) petiolule length of second most distal lateral leaflet (27); (15) petiole wings (31); (16) number of leaflet pairs (9); (17) petiolule length of terminal leaflet (17); (18) most distal lateral leaflet width (18); (19) length from widest point of second most distal lateral leaflet blade to base of blade (25); (20) length from widest point of the terminal leaflet blade to base of blade (15); (21) leaf width (7).

We also used stepwise discriminant analysis to discover characters that best distinguished the nine phenetically most similar primitive Mexican diploid species. This analysis used the 14 morphological characters, arranged from highest to lowest discriminant ability. Nine of these 14 are quantitative character distributions and are graphically displayed in Figure 3, while 5 character state distributions are qualitative: (1) fruit shape: globose in all species except *S. hintonii* and *S. trifidum*, which had conical fruits (56); (2) leaf decurrence: all are laterally decurrent except *S. cardiophyllum* subsp. *ehrenbergii, S. hintonii*, and *S. tarnii*, which are not (30); (3) shape of pseudostipular leaf: lunate in all species except pinnulate in *S. jamesii* (33); (4) only *S. ×michoacanum* and *S. tarnii* lack interstitial leaflets (12); (5) ratio: length of second most distal lateral leaflet blade/width of second most distal lateral leaflet (24); (6) abaxial leaf pubescence length (28); (7) length of calyx acumen (42); (8) petiole length (32); (9) width of second most distal lateral leaflet (23); (10) secondary color of abaxial surface of corolla: 100% white in *S. hintonii*, *S. stenophyllidium*, *S. tarnii*, and *S. trifidum*, only 42.8% white in *S. brachistotrichium* (the rest white with tones of violet), 16.6% white in *S. cardiophyllum* subsp. *ehrenbergii* and *S. jamesii* (the rest white with tones of violet), and 50% white in *S. nayaritense* (the rest white with tones of violet) (54); (11) style exsertion (46); (12) length from widest point of second most distal lateral leaflet blade to base of blade (25); (13) stem diameter (3); (14) number of leaflet pairs (9).

Significant differences in character states for this reduced matrix of nine phenetically most similar primitive Mexican diploid taxa, as determined by the Tukey-Kramer test, found 21 characters (all quantitative) best distinguish these taxa. These 21 characters include all 9 of the quantitative characters mentioned above as determined by STEPDISC. The means, ranges, and standard deviations of these 21 characters are graphically presented in Figure 3. It shows that most of these characters overlap considerably in range, and provide few species-specific character states useful for easy diagnoses of taxa. Some exceptions, however, are low number of lateral leaflet pairs in *S. nayaritense* (character 9), long petiolules (17), long petioles (32), and wide corolla lobes as measured at the base of the corolla junction (51) in *S. hintonii*. This trend of the sole to predominant presence of overlapping character states to define taxa is common in *Solanum* sect. *Petota* (Spooner & van den Berg, 1992; Spooner & Hijmans, 2001), and termed polythetic support. A polythetic morphological species concept is one where species are defined where they have the greatest number of shared features, no single feature of which is essential for group membership or is sufficient to make an organism a member of a group (Sokal & Sneath, 1963; Stuessy, 1990). Stated otherwise, species are distinguished only by a complex set of character states that overlap in ranges.

MICROSATELLITE PHENETICS

Only 12 of the 45 primers we tried, from 8 linkage groups as mapped by Milbourne et al. (1998) for *Solanum tuberosum*, gave useable results. There were amplification failures in these 12 ranging from 4% in stm0003 and stm3009, to 58% in stm0007, with the average across all primers 22% (Table 3). It is frequent in cross-species amplification to reduce the annealing temperature in order to obtain amplification (Ezenwa et al., 1998). A range of up to 5°C less was attempted to achieve amplification when no product otherwise could be obtained, but with futile results. We considered an amplification successful when the positive control (*S. tuberosum*) amplified, as well as most of the primitive Mexican diploids.

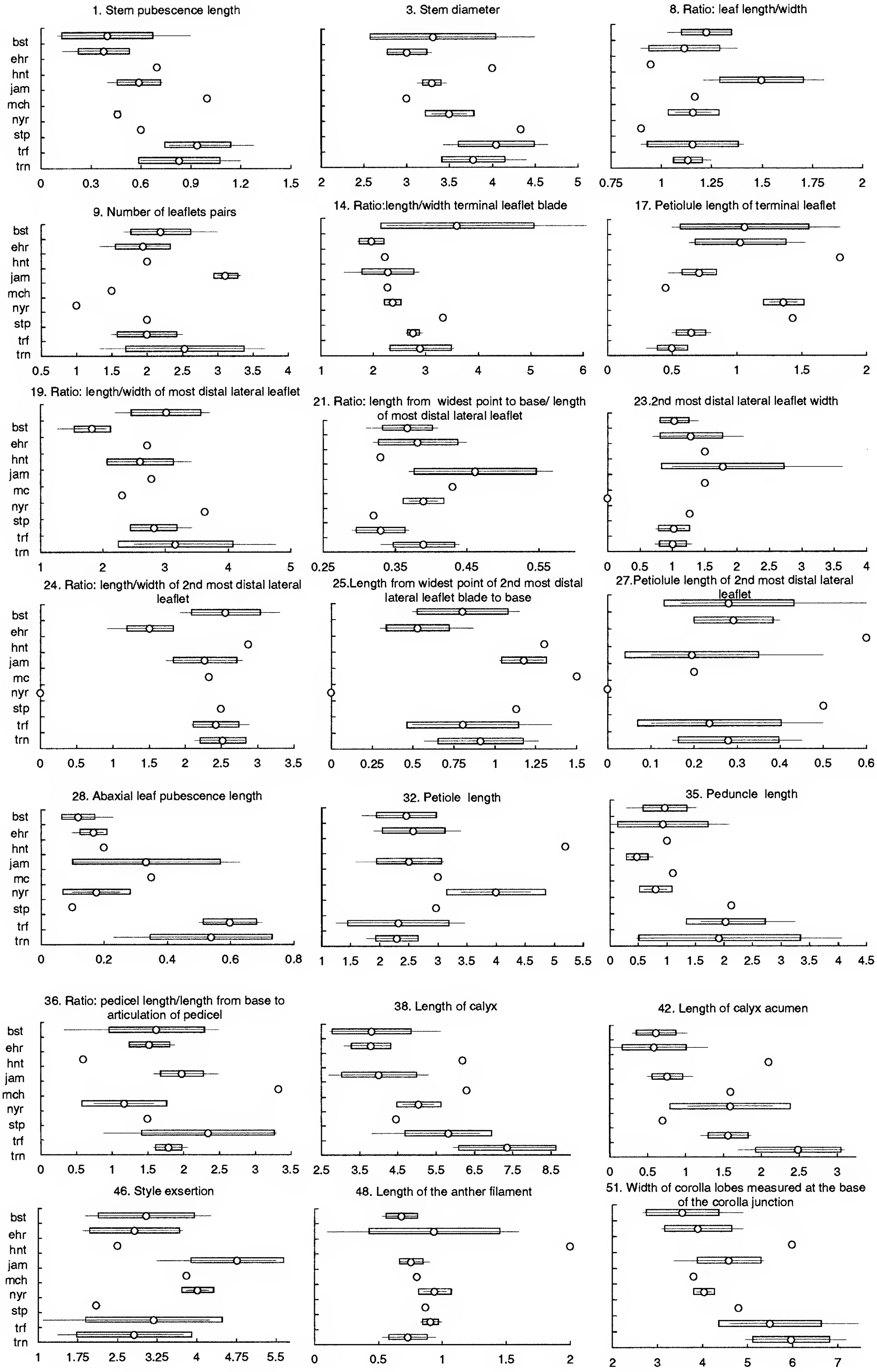

Figure 3. Means (dot), ranges (length of line), and one standard deviation of the mean (length of box) for 21 of the 35 statistically significant morphological characters of the phenetically most similar diploid wild species from the United States, Mexico, and Central America. Included here are only the quantitative characters; the number preceding the character corresponds to Table 2. All measurements are in cm except characters 1, 3, 28, 38, 42, 46, 48, and 51, which are in mm. Three-letter species codes follow Spooner and Hijmans (2001): bst = *S. brachistotrichium;* ehr = *S. cardiophyllum* subsp. *ehrenbergii;* hnt = *S. hintonii;* jam = *S. jamesii;* mch = *S.* ×*michoacanum;* nyr = *S. nayaritense;* stp = *S. stenophyllidium;* trf = *S. trifidum;* trn = *S. tarnii.*

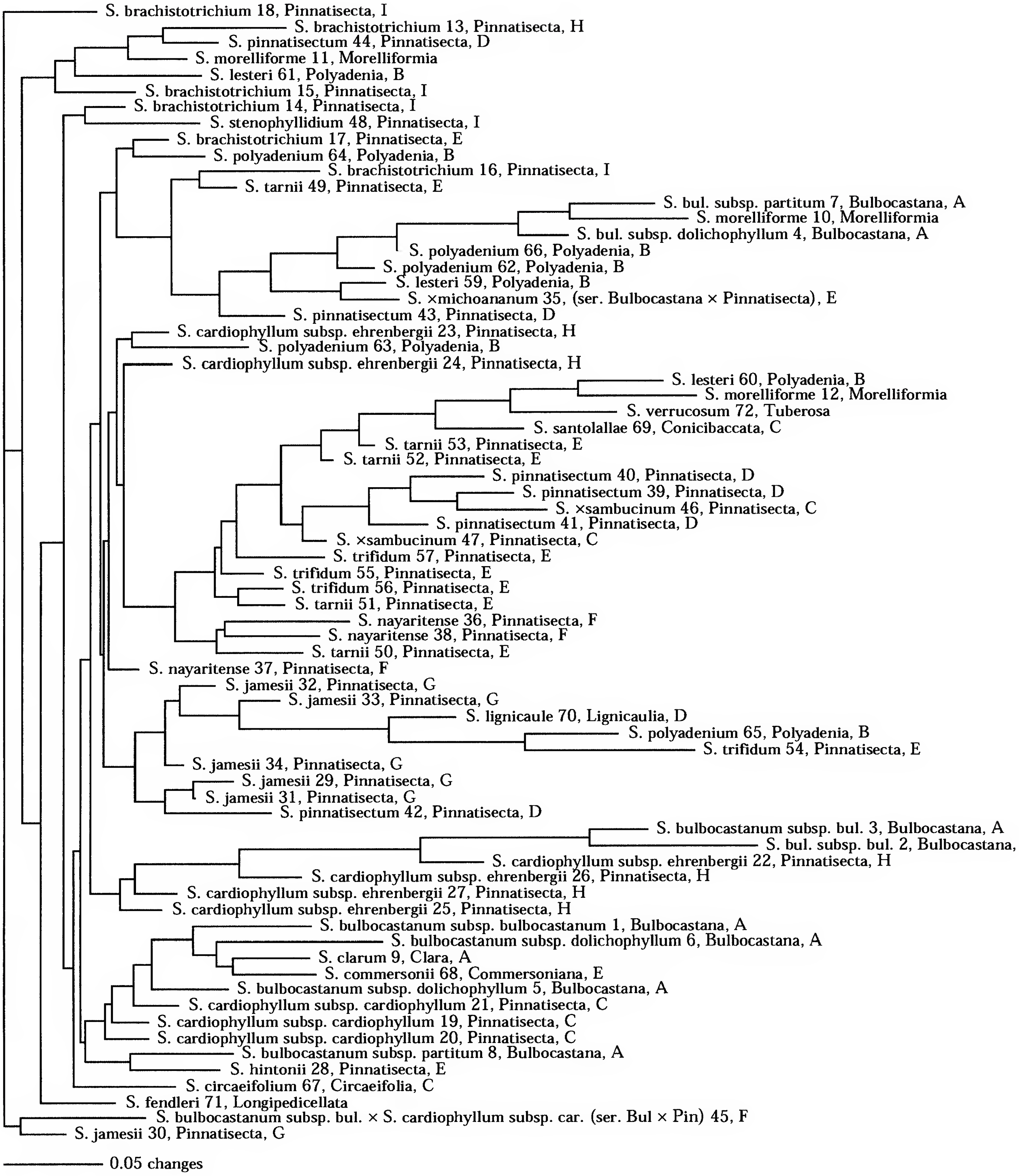
S. brachistotrichium 18, Pinnatisecta, I
S. brachistotrichium 13, Pinnatisecta, H
S. pinnatisectum 44, Pinnatisecta, D
S. morelliforme 11, Morelliformia
S. lesteri 61, Polyadenia, B
S. brachistotrichium 15, Pinnatisecta, I
S. brachistotrichium 14, Pinnatisecta, I
S. stenophyllidium 48, Pinnatisecta, I
S. brachistotrichium 17, Pinnatisecta, E
S. polyadenium 64, Polyadenia, B
S. brachistotrichium 16, Pinnatisecta, I
S. tarnii 49, Pinnatisecta, E
S. bul. subsp. partitum 7, Bulbocastana, A
S. morelliforme 10, Morelliformia
S. bul. subsp. dolichophyllum 4, Bulbocastana, A
S. polyadenium 66, Polyadenia, B
S. polyadenium 62, Polyadenia, B
S. lesteri 59, Polyadenia, B
S. ×michoananum 35, (ser. Bulbocastana × Pinnatisecta), E
S. pinnatisectum 43, Pinnatisecta, D
S. cardiophyllum subsp. ehrenbergii 23, Pinnatisecta, H
S. polyadenium 63, Polyadenia, B
S. cardiophyllum subsp. ehrenbergii 24, Pinnatisecta, H
S. lesteri 60, Polyadenia, B
S. morelliforme 12, Morelliformia
S. verrucosum 72, Tuberosa
S. santolallae 69, Conicibaccata, C
S. tarnii 53, Pinnatisecta, E
S. tarnii 52, Pinnatisecta, E
S. pinnatisectum 40, Pinnatisecta, D
S. pinnatisectum 39, Pinnatisecta, D
S. ×sambucinum 46, Pinnatisecta, C
S. pinnatisectum 41, Pinnatisecta, D
S. ×sambucinum 47, Pinnatisecta, C
S. trifidum 57, Pinnatisecta, E
S. trifidum 55, Pinnatisecta, E
S. trifidum 56, Pinnatisecta, E
S. tarnii 51, Pinnatisecta, E
S. nayaritense 36, Pinnatisecta, F
S. nayaritense 38, Pinnatisecta, F
S. tarnii 50, Pinnatisecta, E
S. nayaritense 37, Pinnatisecta, F
S. jamesii 32, Pinnatisecta, G
S. jamesii 33, Pinnatisecta, G
S. lignicaule 70, Lignicaulia, D
S. polyadenium 65, Polyadenia, B
S. trifidum 54, Pinnatisecta, E
S. jamesii 34, Pinnatisecta, G
S. jamesii 29, Pinnatisecta, G
S. jamesii 31, Pinnatisecta, G
S. pinnatisectum 42, Pinnatisecta, D
S. bulbocastanum subsp. bul. 3, Bulbocastana, A
S. bul. subsp. bul. 2, Bulbocastana,
S. cardiophyllum subsp. ehrenbergii 22, Pinnatisecta, H
S. cardiophyllum subsp. ehrenbergii 26, Pinnatisecta, H
S. cardiophyllum subsp. ehrenbergii 27, Pinnatisecta, H
S. cardiophyllum subsp. ehrenbergii 25, Pinnatisecta, H
S. bulbocastanum subsp. bulbocastanum 1, Bulbocastana, A
S. bulbocastanum subsp. dolichophyllum 6, Bulbocastana, A
S. clarum 9, Clara, A
S. commersonii 68, Commersoniana, E
S. bulbocastanum subsp. dolichophyllum 5, Bulbocastana, A
S. cardiophyllum subsp. cardiophyllum 21, Pinnatisecta, C
S. cardiophyllum subsp. cardiophyllum 19, Pinnatisecta, C
S. cardiophyllum subsp. cardiophyllum 20, Pinnatisecta, C
S. bulbocastanum subsp. partitum 8, Bulbocastana, A
S. hintonii 28, Pinnatisecta, E
S. circaeifolium 67, Circaeifolia, C
S. fendleri 71, Longipedicellata
S. bulbocastanum subsp. bul. × S. cardiophyllum subsp. car. (ser. Bul × Pin) 45, F
S. jamesii 30, Pinnatisecta, G
0.05 changes

Figure 4. Neighbor-joining dendrogram based on microsatellite data (Nei & Li, 1979, similarity). Species names and accession numbers as in Table 1 and Figures 1 and 2, and phenetic groups from Figure 2.

The trees obtained from the two stepwise mutation model (SMM) matrices showed little to no concordance with the morphology phenogram, that is, they failed to cluster well-defined morphological species (trees not presented). The infinite allele model (IAM) with UPGMA and NJ clustered taxa somewhat better but still very poorly relative to the morphology phenogram (Fig. 2). Our first analysis included all taxa, and NJ clustered taxa best (shown in Fig. 4), but still only provided weak clustering of some accessions of some species (such as a partial clustering of *Solanum cardiophyllum* subsp. *cardiophyllum*, *S. jamesii*, and *S. nayaritense*, all members of ser. *Pinnatisecta*), but with failure to completely cluster these and most other species. To attempt better clustering of putatively related taxa, we analyzed just the most phenetically similar primitive Mexican diploids *S. brachistotrichium*, *S. cardiophyllum* subsp. *cardiophyllum*, subspecies *ehrenbergii*, *S. nayaritense*, and *S. stenophyllidium* (all within ser. *Pinnatisecta*). This reduced analysis (not presented) still intermixed accessions of all species except for *S. cardiophyllum* subsp. *cardiophyllum* as in Figure 4; that is, it still showed little to no species-specific clustering. Microsatellites also were of no use to investigate hybrid origins of *S.* ×*michoacanum*, *S.* ×*sambucinum*, and the putative hybrid *S. bulbocastanum* × *S. cardiophyllum* (Rodríguez & Vargas-P., 1994). There were no additive species-specific bands present to test these hypotheses.

DISCUSSION

CONCORDANCE OF MORPHOLOGICAL DATA WITH PRIOR HYPOTHESES OF RELATIONSHIPS AND CHLOROPLAST DNA DATA

Our morphological results show areas of concordance and discordance with cpDNA results of Spooner and Sytsma (1992), Rodríguez and Spooner (1997), and with prior hypotheses of interspecific relationships (Hawkes, 1989, 1990; Hawkes et al., 1988; Hawkes & Jackson, 1992). For example, all members of *Solanum* ser. *Bulbocastana* are well resolved and separated from the rest of the Mexican diploids (Fig. 2, cluster A). However, *S. bulbocastanum* subsp. *bulbocastanum* was the only subspecies relatively well supported, not *S. bulbocastanum* subsp. *dolichophyllum* and subspecies *partitum*. Our morphological data also unite *S. bulbocastanum* and *S. clarum*, supporting Hawkes (1990) who united them in *Solanum* ser. *Bulbocastana*. Chloroplast DNA data (Spooner & Sytsma, 1992; Rodríguez & Spooner, 1997), however, supported the sister-taxon relationship of *S. bulbocastanum* and *S. cardiophyllum* (Fig. 2, clusters A and C, in part), not *S. bulbocastanum* and *S. clarum*.

Solanum lesteri and *S. polyadenium* (cluster B) form a good phenetic group, concordant with cpDNA results (Spooner & Sytsma, 1992) and Hawkes's (1990) placement in *Solanum* ser. *Polyadenia*. *Solanum* ×*sambucinum* clusters with neither of its putative parents (*S. cardiophyllum* subsp. *ehrenbergii* and *S. pinnatisectum*). *Solanum trifidum* and *S. tarnii* (both ser. *Pinnatisecta*) also form a good phenetic group (cluster E), concordant with cpDNA data, and recognition of their phenetic similarity by Hawkes et al. (1988). Although not examined for cpDNA, Hawkes (1990) intuitively noted a morphological similarity of *S. hintonii* and *S. trifidum*, concordant with our data (cluster E).

The cluster of *Solanum nayaritense* with the putative hybrid of *S. bulbocastanum* × *S. cardiophyllum* (cluster F) is discordant with morphological interpretations (Rodríguez et al., 1995) as *S. nayaritense* has not been suggested as its progenitor. The phenetic relationship of *S. jamesii* (cluster G) and *S. cardiophyllum* subsp. *ehrenbergii* (cluster H) has never been suggested before, but is reasonable based on cpDNA results that show them to be part of the same clade (Spooner & Sytsma, 1992; Rodríguez & Spooner, 1997). The phenetic separation of *S. cardiophyllum* subsp. *ehrenbergii* (cluster H) from subspecies *cardiophyllum* (cluster C) is concordant with cpDNA data (Rodríguez & Spooner, 1997). The phenetic similarity of *S. brachistotrichium* and *S. stenophyllidium* (cluster I) also has support with cpDNA data (Spooner & Sytsma, 1992), which places them on the same clade.

MICROSATELLITE DATA ANALYSIS

There are two divergent hypotheses of microsatellite evolution and its reflection on best analytical methods for assessment of genetic distances and phylogeny. Schlötterer and Tautz (1992) have shown slippage during replication, which would support the use of the simple mutation model (SMM) for analyses. However, Colson and Goldstein (1999) studied microsatellite loci in *Drosophila* and found that many mutation events in microsatellites are more complex than assumed by SMM. They advised the use of sequence data to assess the accumulation of imperfections within the microsatellite repeat, reducing the number of consecutive repeats. These imperfections can be insertions, deletions, or base substitutions, which, along with stepwise mutation drift to smaller sizes, have contributed to degradation of microsatellite loci over time. The authors caution against the use of microsatellite size alone for population or phylogenetic relationships (Colson & Goldstein, 1999). The SMM has been supported by phylogeny reconstructions in bovine species (MacHugh et al., 1997), fish (Ruzzante, 1998), and human populations (Valdes et al., 1993; Shriver et al., 1995; Kimmel et al., 1996). On the other hand, the infinite allele model (IAM) has been supported for data sets with numerous compound microsatellites (Estoup et al., 1995), which would be the case in our data set. In this study, the best concordance with morphological data was produced with the IAM and the worst with the SMM, but both were very poor. The IAM was the most useful in analyzing subspecies differences in *S. tuberosum* (Raker & Spooner, 2002).

MICROSATELLITE CROSS-SPECIES AMPLIFICATION

Microsatellites are expensive to develop. One of their appealing features is their potential use in related groups beyond the mainly economic plants where they were developed. There are several examples of successful amplification across species. Microsatellites distinguished two closely related species in genus *Sitobion* (Hemiptera: Aphidoidea) (Figueroa et al., 1999). Microsatellites developed for the tropical tree *Pithecellobium elegans* were conserved in several species of the tribe Ingeae (Dayanandan et al., 1997). Microsatellites from peach successfully amplified fragments in apple, suggesting that they might be useful as well in other fruit crops (Cipriani et al., 1999). In the genus *Dianthus*, microsatellite loci developed from the EMBL database were tested in 26 species within the genus, and successful amplification implied that the species are closely related or that the primer regions are well conserved (Smulders et al., 2000). Eight of 17 microsatellite primer pairs designed for *Quercus petraea* were successful in producing amplifications in the related genus *Castanea*, and 4 of the 17 in *Fagus*. Twelve of these 136 amplifications were cloned and sequenced and shown to be homologous to *Quercus petraea*; nevertheless, the authors recognized a tendency for decreasing ability to successfully amplify loci, with increasing evolutionary distance across the family (Steinkellner et al., 1997). The same relationship between an increasing genetic distance and decreasing success of microsatellite amplification was observed in cassava (*Manihot esculenta* Crantz), through tests with six *Manihot* wild species (Roa et al., 2000).

In addition to problems producing microsatellite fragments across species, there also are problems with homology of the microsatellite fragment that is necessary for correct phylogenetic interpretations (Wendel & Doyle, 1998). For successful amplification of homologous fragments the target sequence for the primers *and* flanking sequence about the microsatellites must be sufficiently conserved (Ezenwa et al., 1998). Knowledge of these criteria is costly as it requires sequencing the PCR fragments.

In our study the primers were developed through a Genbank search of *Solanum tuberosum* (Milbourne et al., 1998). Chloroplast DNA data (Spooner & Sytsma, 1992) show the primitive Mexican diploids to be the most distantly related group to *S. tuberosum* in section *Petota*, and microsatellites performed poorly for phylogenetic reconstructions. Similar problems have been found in other groups. Sequence variation and/or variation in the number of repeats has been found by Peakall et al. (1998), who used 31 soybean microsatellite loci in wild relatives and found that cross-species amplification was low, mainly in closely related genera. When cross-species amplification was achieved there was sequence variation in the flanking regions and within the repeats (non-homologous amplification). Westman and Kresovich (1998) tried to use *Arabidopsis* primer pairs to amplify microsatellites in the closely related genus *Brassica*, but many amplified loci did not hybridize with microsatellite probes, and probably did not contain repeats. In animals, microsatellites derived from two species of wasps successfully cross-species amplified in different related genera from the Vespidae. However, the loci from one species were more conserved than those from the other, warning that it is difficult to reach generalizations regarding conservation rates using data from single species (Ezenwa et al., 1998). In avian microsatellites, 73 primer sets from 16 species across nine families were tested on *Quelea* species. Only 22 of these 73 pairs produced homologous amplification (Dallimer, 1999).

The issue of cross-species amplification is complex. As seen above, it can be achieved across genera within families, or not even occur across species within a genus. To our knowledge there is no comprehensive summary that addresses the comparative extent of microsatellite conservation or whether the failure of cross-species amplification is due to primer design or phylogenetic distance. Clisson et al. (2000) sequenced primate microsatellites with primers designed in humans and found that alterations in the base composition of repeats, and insertions and deletions in flanking regions, are important components of the variation but introduced homoplasy (same size but different composition) reducing their phylogenetic utility.

CONCLUSIONS

Most of the species examined in our study were supported by morphological characters, except *Solanum brachistotrichium* and possibly *S. stenophyllidium*. However, microsatellites provided poor to no support for species. This could be caused by non-homology of repeat length between the primers, or in our study by not having enough data to provide phylogenetic signal. There continue to be unanswered questions about microsatellites regarding mutation processes, proper analytical tools for phylogeny, and knowledge of the extent of cross-species amplification. Our results show that microsatellites developed from *S. tuberosum* have reduced utility to establish good morphological species from the phylogenetically distant United States, Mexican, and Central American diploid wild potato species. Lara-Cabrera and Spooner (2004) addressed the validity of these species and their interrelationships with AFLP data.

NOTE IN PROOF

These results, and those of Lara-Cabrera and Spooner (2004), were instrumental in revising the wild potatoes of North and Central America (Spooner et al., 2004).

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MORPHOLOGICAL CHARACTERIZATION AND RELATIONSHIPS OF WILD TOMATOES (*SOLANUM* L. SECT. *LYCOPERSICON*)

Iris E. Peralta and David M. Spooner

Abstract. Wild tomatoes (*Solanum* L. sect. *Lycopersicon* (Mill.) Wettst.) are native to western South America. Different classifications have been based on morphological or biological species concepts. Molecular data from mitochondrial DNA restriction sites, nuclear and chloroplast DNA restriction length fragment polymorphisms, and most recently gene sequences of the single-copy nuclear GBSSI or *waxy* gene, also have been used to examine species relationships. This study is a companion to the GBSSI gene sequence study of the same accessions. It provides the first explicit use of morphological data to examine distinctness and relationships of all 10 wild tomato species (including the newly described *S. galapagense*), with a concentration on accessions of the most widespread and variable species, *S. peruvianum*. Phenetic and cladistic analyses largely support the nine species outlined by the latest treatment by C. Rick, but demonstrate the distinct nature of the northern and southern Peruvian populations of *S. peruvianum*, and suggest that they may represent distinct species.

Key words: phylogeny, *Solanum* sect. *Lycopersicon,* tomato.

Wild tomatoes are mainly characterized by anthers with sterile appendages, laterally connivent forming a flask-shaped cone. All species are native to western South America and distributed from central Ecuador, through Peru to northern Chile, and in the Galápagos Islands, where two endemic species, *S. cheesmaniae* and *S. galapagense,* grow (Darwin et al., 2003). Wild tomato species grow in a variety of habitats, from near sea level along the arid Pacific coast to over 3300 m in the numerous valleys of the western side of the Andes (Rick, 1973; Taylor, 1986). The wild ancestor of cultivated tomatoes, *S. lycopersicum*, is more widespread and perhaps more recently distributed into Mexico, Colombia, Bolivia, and other South American countries (Rick & Holle, 1990). Wild species provide a wealth of useful genetic traits to improve cultivated tomatoes. The traditional breeding for pure lines in the crop has contributed to its narrow genetic base (Stevens & Rick, 1986). All wild tomato species are diploids ($2n = 2x = 24$) and can be crossed (but sometimes with difficulty) to the cultivated tomato. They are of great use in breeding programs as sources of disease resistance and agronomic traits (Esquinas Alcazar, 1981; Laterrot, 1989; Rick, 1982a, 1986a, 1987; Rick et al., 1987; Stevens & Rick, 1986). The tomato also serves as a model organism for genetic studies (Tanksley & McCouch, 1997; Hay et al., 2004).

Wild tomatoes exhibit great differences in morphological characters, mating systems, and habitat preferences. In their natural habitats, wild tomatoes probably behave as annuals because frost or drought kills the plants after the first growing season, but they can be biennial or perennial herbs (Müller, 1940). All tomato species are pubescent, and trichome types and density are valuable characters to distinguish species. Stems are slender and herbaceous throughout, but also can undergo secondary growth at the base. Habits vary from erect to procumbent to decumbent. Leaves are alternate, imparipinnate to bipinnate, with 2 to 6 opposite or sub-opposite pairs of petiolate or subsessile leaflets, and sometimes with additional small sessile or subsessile interjected leaflets. Leaf dissection distinguishes subspecies or varieties of *S. peruvianum*. The basic inflorescence includes monochasial, dichotomous, and polychotomous cymes (Luckwill, 1943). Some wild tomato species develop inflorescence bracts and pseudostipules at the base of the leaf petiole. Flowers are typically yellow, the calyx is divided in five lobes that are accrescent about the fruits, and the corolla is stellate or stellate-rotate. The five anthers have an elongated sterile appendage at the apex and are laterally connivent forming a flask-shaped cone, except in *S. pennellii*. Fruits are fleshy berries with two or rarely more locules, variable in size, shape, color, and pubescence.

Müller (1940) and Luckwill (1943) produced the two most recent and complete taxonomic treatments of wild tomatoes based on morphological concepts, and treated them under *Lycopersicon* (Fig. 1). Müller (1940) divided the genus into two subgenera: (1) *Eulycopersicon* C. H. Müll., with two species possessing glabrous, and red- to orange- to yellow-colored fruits; flat and silky pubescent seeds; bractless inflorescences; and leaves without pseudostipules; and (2) *Eriopersicon* C. H. Müll., with four species bearing pubescent green or greenish white to yellowish and purple tinged fruits, frequently with a dark green, lavender, or purple stripe; thick glabrous seeds or pilose only at the apex; bracteate inflorescences; and leaves usually with pseudostipules. Müller (1940) also described *L. glandulosum* C. H. Müll. and classified the highly polymorphic *L. peruvianum* into two varieties: var. *dentatum* Dunal and var. *humifusum* C. H. Müll.

Luckwill (1943; Fig. 1) adopted the two subgenera recognized by Müller (1940) and proposed a phylogeny of *Lycopersicon*. He hypothesized that the two subgenera might have evolved from an ancestral simple form characterized by imparipinnate leaves with 5 to 7 entire leaflets, few interjected leaflets, and probably no secondary leaflets, unbranched inflorescences, and

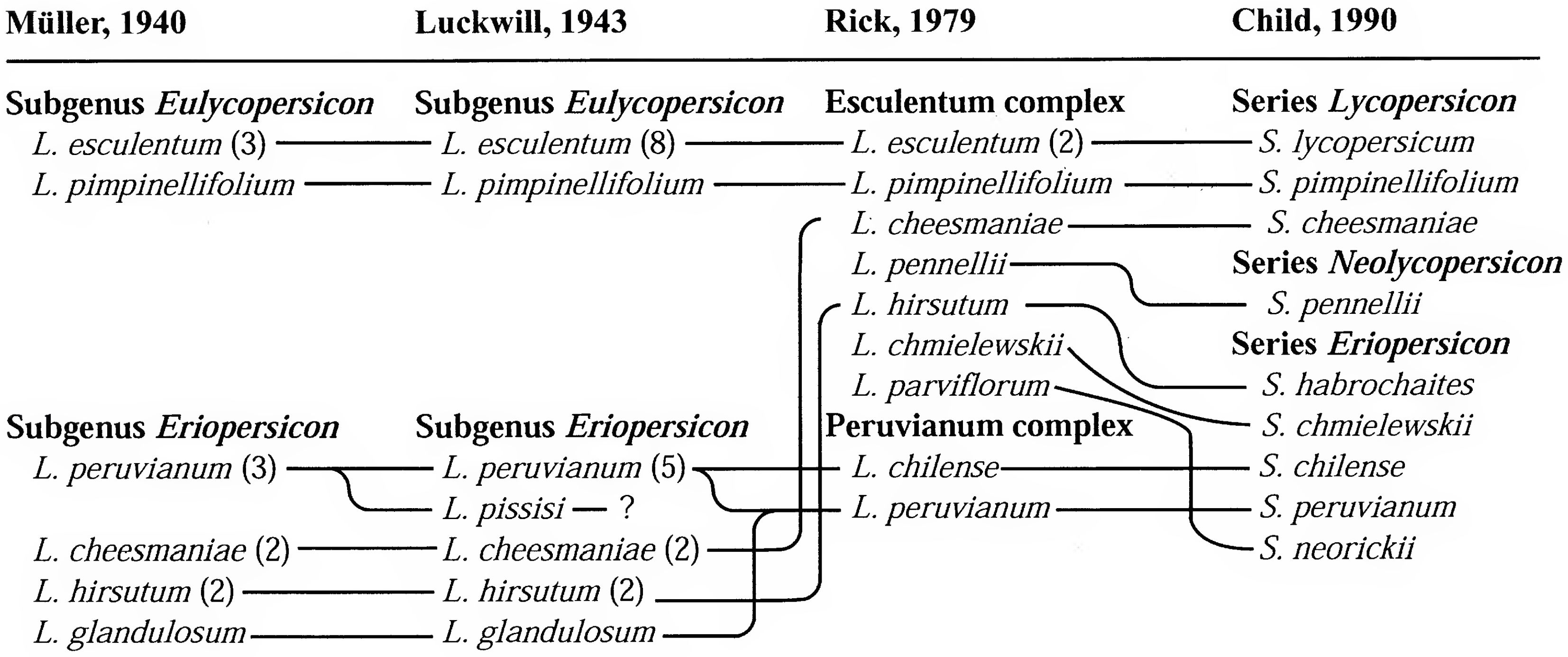
Müller, 1940
Luckwill, 1943
Rick, 1979
Child, 1990
Subgenus Eulycopersicon
L. esculentum (3)
L. pimpinellifolium
Subgenus Eriopersicon
L. peruvianum (3)
L. cheesmaniae (2)
L. hirsutum (2)
L. glandulosum
Subgenus Eulycopersicon
L. esculentum (8)
L. pimpinellifolium
Subgenus Eriopersicon
L. peruvianum (5)
L. pissisi — ?
L. cheesmaniae (2)
L. hirsutum (2)
L. glandulosum
Esculentum complex
L. esculentum (2)
L. pimpinellifolium
L. cheesmaniae
L. pennellii
L. hirsutum
L. chmielewskii
L. parviflorum
Peruvianum complex
L. chilense
L. peruvianum
Series Lycopersicon
S. lycopersicum
S. pimpinellifolium
S. cheesmaniae
Series Neolycopersicon
S. pennellii
Series Eriopersicon
S. habrochaites
S. chmielewskii
S. chilense
S. peruvianum
S. neorickii

Figure 1. Comparison of classifications of *Solanum* sect. *Lycopersicon.* The numbers in parentheses represent numbers of infraspecific ranks (subspecies, varieties, and forms). The lines connect synonymous taxa.

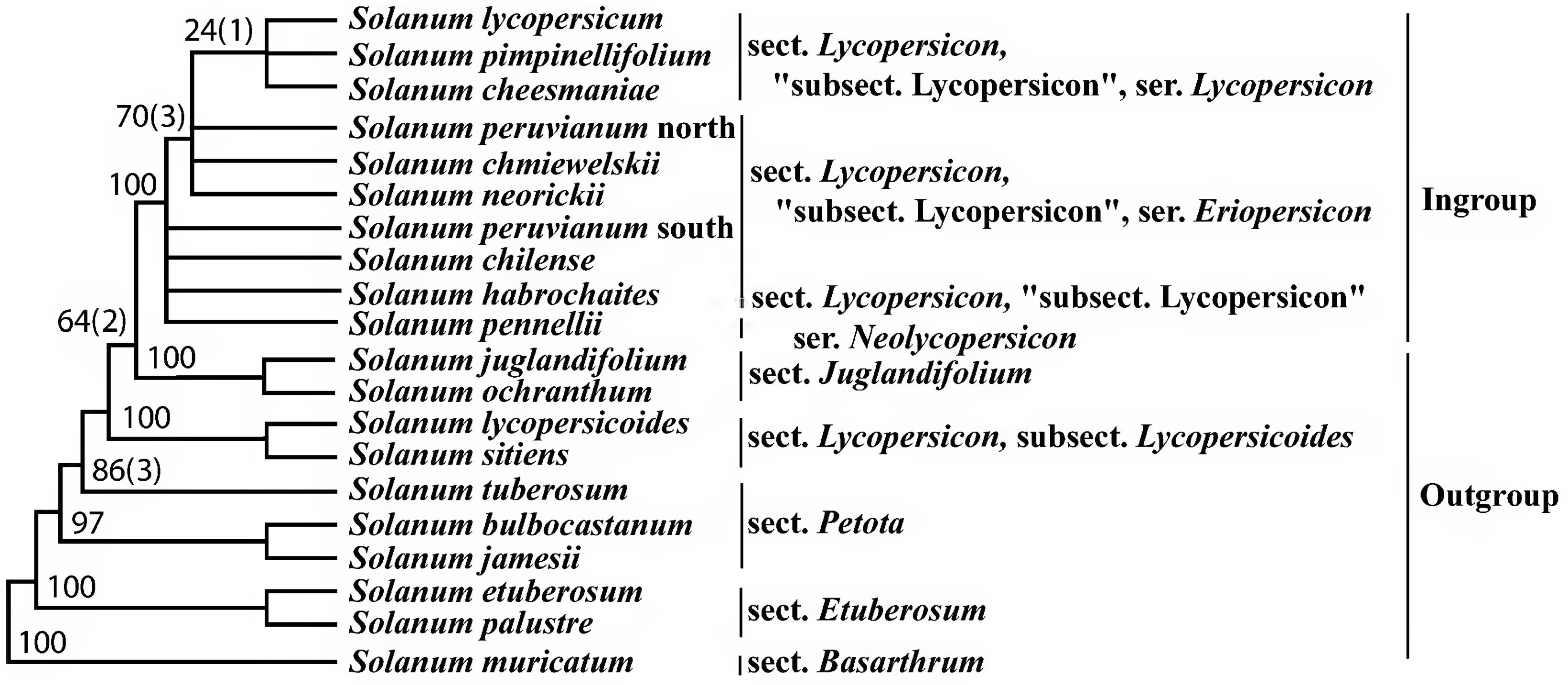
24(1)
70(3)
100
64(2)
100
100
86(3)
97
100
100
Solanum lycopersicum
Solanum pimpinellifolium
Solanum cheesmaniae
Solanum peruvianum north
Solanum chmiewelskii
Solanum neorickii
Solanum peruvianum south
Solanum chilense
Solanum habrochaites
Solanum pennellii
Solanum juglandifolium
Solanum ochranthum
Solanum lycopersicoides
Solanum sitiens
Solanum tuberosum
Solanum bulbocastanum
Solanum jamesii
Solanum etuberosum
Solanum palustre
Solanum muricatum
sect. Lycopersicon, "subsect. Lycopersicon", ser. Lycopersicon
sect. Lycopersicon, "subsect. Lycopersicon", ser. Eriopersicon
sect. Lycopersicon, "subsect. Lycopersicon" ser. Neolycopersicon
sect. Juglandifolium
sect. Lycopersicon, subsect. Lycopersicoides
sect. Petota
sect. Etuberosum
sect. Basarthrum
Ingroup
Outgroup

Figure 2. Abstracted cladistic results of the 65 accessions of the 9 tomato species and 14 outgroup taxa examined in the phylogenetic analysis of the GBSSI gene sequences by Peralta and Spooner (2001). Nomenclature of *Solanum* subg. *Potatoe* according to Child (1990). We here informally label wild tomatoes in the clade containing all members of "subsect. Lycopersicon" (*S. lycopersicum* to *S. pennellii*) to provide a coordinate name for their formally described outgroups in section *Juglandifolium* (Rydb.) Child and subsection *Lycopersicoides* Child. Our use of these ranks may change in our monograph of tomatoes and their relatives (Peralta et al., in prep.). Numbers indicate bootstrap values, and decay values are indicated between parentheses.

undeveloped pseudostipules. Two different lineages diverged from the ancestral forms, one characterized by fruits with carotenoid pigments and the other by green fruits with anthocyanin pigments. Luckwill (1943) agreed with Müller (1940) in the circumscription of subgenus *Eulycopersicon*, but within *Eriopersicon* he considered *L. pissisi* a distinct species, with *L. peruvianum* var. *humifusum* C. H. Müll. as its basionym (Fig. 1). He also proposed different infraspecific categories in *L. esculentum*, *L. cheesmaniae*, and *L. peruvianum*. *Lycopersicon cheesmaniae*, with yellow to orange fruits, bractless inflorescences, and leaves without pseudostipules, apparently was misclassified in the subgenus *Eriopersicon* by Müller (1940) and Luckwill (1943).

D'Arcy (1972) treated tomatoes in the genus *Lycopersicon* but did not address subgeneric relationships. More recently, Child (1990, Fig. 1) placed tomatoes in *Solanum* subg. *Potatoe* (G. Don) D'Arcy, sect. *Lycopersicon* (Mill.) Wettst., subsect. *Lycopersicon*, mainly characterized by anthers with sterile appendages and laterally connivent forming a tube, and classified them in three series: *Lycopersicon*, *Eriopersicon* (C. H. Müll.) Child, and *Neolycopersicon* (Correll) Child (Fig. 1). The first two series correspond to the subgenera *Eulycopersicon* and *Eriopersicon* used by Müller (1940) and Luckwill (1943). Series *Lycopersicon* includes herbs with few or no pseudostipules, ebracteate inflorescences, and fruits with carotenoid pigments, and *Eriopersicon* includes herbs to subshrubs with pseudostipules, bracteate inflorescences, and fruits with no carotenoid pigments (fruits pure green or greenish white, dark green to purple striped). Series *Neolycopersicon* only includes *S. pennellii* (Correll, 1958), a species with curved, markedly unequal length anthers loosely coherent and without sterile appendages. Child (1990) also proposed *Solanum* sect. *Lycopersicon* (Mill.) Wettst., subsection *Lycopersicoides* Child, and section *Juglandifolium* (Rydb.) Child as the closest relatives of subsection *Lycopersicon*.

Most recently, a new orange-fruited species of tomato was recognized, *S. galapagense* S. Darwin & Peralta (Darwin et al., 2003). Within tomatoes it shares its orange fruit color only with *S. cheesmaniae*, but is clearly distinguished from it by a number of leaf and flower traits. This species, formerly recognized as *S. cheesmaniae* f. *minor*, is clearly related to the other species with carotenoid pigments and is included in the present study.

Mating systems have played an important role in the evolution of wild tomato species, varying from allogamous self-incompatible, to facultative allogamous and self-compatible, to autogamous and self-compatible (Rick, 1963, 1979, 1982b, 1986b; Table 1). The self-incompatibility system in tomatoes is gametophytic and controlled by a single, multiallelic S locus (Tanksley & Loaiza-Figueroa, 1985).

The self-incompatibility system has shown strong relationships between the extent of outcrossing and allelic polymorphisms, floral display, and degree of stigma exsertion in wild tomatoes. Rick (1982b) investigated the genetic bases of self-compatibility, self-incompatibility, and flower characters, using interspecific hybrids between the self-compatible (SC) *S. pimpinellifolium*, used as recurrent parent, and the two self-incompatible (SI) species, *S. habrochaites* and *S. pennellii*. He postulated that three independent genetic phases, most probably regulated by different unlinked genes or gene complexes, are essential for successful functioning of the self-incompatibility system. These genes are operating on (1) prevention of self-fertilization, (2) changes in the flower organs to ensure cross-pollination, and (3) development of secondary flower characters to attract pollinators. He concluded that the evolution of a mating system in wild tomatoes has occurred from self-incompatibility, as ancestral condition, to self-compatibility, and probably never reversed to self-incompatibility. Changes from self-incompatibility to self-compatibility are expected to arise frequently and independently (Rick, 1982b). This trend has been found in *S. habrochaites* and *S. pennellii*, both with self-incompatible and self-compatible populations. The self-incompatible populations occupy the center of their species geographic distributions, and have higher genetic variation, larger flower parts, and exserted stigmas. Self-compatible populations occur toward the northern and southern edges of *S. habrochaites* and *S. pennellii* distribution, have less genetic variation, smaller flower parts, and little or no stigma exsertion (Rick et al., 1979; Rick & Tanksley, 1981). The change from self-incompatibility to self-compatibility has been reported in only one population of *S. peruvianum* (Rick, 1986b).

In the self-compatible species, the extent of outcrossing and genetic variation is also related to floral display and degree of stigma exsertion. Marginal populations of *Solanum pimpinellifolium* are highly autogamous with little or no genetic variation, small flower parts, and little or no stigma exsertion, while the central facultative allogamous populations have high genetic variation, larger corollas, and marked stigma exsertion (Rick et al., 1977). A comparison of different *S. pimpinellifolium* genotypes in experimental plots in Peru showed that different outcrossing rates could be largely attributed to differences in floral characters, especially the level of stigma exsertion, rather than to differences in numbers and types of pollinators (Rick et al., 1978).

Two closely related self-compatible species, *S. chmielewskii* and *S. neorickii*, illustrate another example of changes in flower characters associated with outcrossing and genetic variation. *Solanum neorickii* is exclusively autogamous with low intra-population genetic variation and small flowers with stigmas included in the anther tube. In contrast, the facultative allogamous *S. chmielewskii* exhibited higher levels of heterozygosity, larger flower parts, and exserted stigmas. Rick et al. (1976) postulated that *S. neorickii* evolved from *S. chmielewskii*. All populations of *S. chilense* are self-incompatible. The related species *S. lycopersicoides*, *S. sitiens*, *S. ochranthum*, and *S. juglandifolium* are exclusively self-incompatible.

In contrast to the morphological species concepts of Müller (1940) and Luckwill (1943), Rick (1960, 1963, 1979, 1986b) recognized species and proposed a supraspecific classification based primarily on the biological criteria of mating systems, cytology, genetic variation, and crossing relationships. He recognized nine species of *Lycopersicon* (Fig. 1; Rick, 1979), including two new species, *L. parviflorum* and *L. chmielewskii* (Rick et al., 1976), and *L. pennellii* (Rick, 1979). Furthermore, *L. chilense*, a species described by Dunal (1852), was revalidated by Rick and Lamm (1955), and *L. glandulosum* was included as a synonym of *L. peruvianum*.

In order to determine the crossing relationships necessary for his tomato breeding program, Rick (1963, 1979, 1986b) hybridized numerous accessions of all tomato species in all possible combinations and found two major crossing complexes. The Esculentum complex included seven species, mainly self-compatible and intercrossable (Fig. 1; Table 1). *Lycopersicon hirsutum* and *L. pennellii* typically are self-incompatible, but with some self-compatible populations. Three species of the Esculentum complex have mostly glabrous, red- to orange- to yellow-colored fruits (*L. cheesmaniae*, *L. esculentum*, *L. pimpinellifolium*), while the others have pubescent, green fruits (*L. chmielewskii*, *L. hirsutum*, *L. parviflorum*, *L. pennellii*). Hybrids were obtained in all combinations, in spite of the presence of some unilateral incompatibility. The Peruvianum complex, on the other hand, included the self-incompatible species *L. chilense* and *L. peruvianum* (Fig. 1; Table 1), both with pubescent green fruits. The barrier between these two complexes can be broken only by embryo rescue (Rick, 1979). The chromosomes of the F_1 hybrids of successful intercomplex crosses generally showed complete pairing at pachytene, and normal chiasmata formation and chromosome segregation at anaphase during meiosis. Rick (1979) concluded that speciation in wild tomatoes took place mainly via gene substitution and, to a minor extent, by chromosomal differentiation. He also pointed out that natural hybridization is very

TABLE 1.

Accessions of wild tomatoes and outgroups, examined for morphological (this paper) and GBBSI gene sequence variation (Peralta & Spooner, 2001). Vouchers are deposited at BM, MERL, PTIS, and WIS. We used the *Solanum* equivalents of the *Lycopersicon* species as recognized by Rick et al. (1990), with the addition of the varieties and forms of *S. habrochaites*, *S. pennellii*, and *S. peruvianum* as listed in the database of germplasm at the C. M. Rick Tomato Genetics Resource Center (<http://tgrc.ucdavis.edu>).

Taxon[a]	Map Locality[b]	Accession Number[c]	Collector[d]	Breeding System[e]	Locality[f]
Ingroup, *Solanum* sect. *Lycopersicon*					
chs	G	LA166	Unknown	Aut-SC	Ecuador. Galápagos Islands: Santa Cruz, Barranco, N of Punta Ayora, 1 km N of Punta Ayora, 50 m
chs	G	LA1450	Unknown	Aut-SC	Ecuador. Galápagos Islands: Isabela, Bahia San Pedro, 1/2 km from coast, 15 m
gal	G	LA317	Unknown	Aut-SC	Ecuador. Galápagos Islands: Bartolome, 15 m
chl	29	LA1930	*Rick et al. 3172*	Allo-SI	Peru. Arequipa: Quebrada Calapampa, Río Acarí, 500 m, 15°39'S, 74°39'W
chl	36	LA1963	*Rick et al. 3204*	Allo-SI	Peru. Tacna: Río Caplina, 13 km W of Tacna, 3 km from Panamerican Hwy., toward Boca del Río, 200 m, 18°14'S, 70°33'W
chl	38	LA2884	*Rick et al. 7609*	Allo-SI	Chile. Antofagasta: Ayaviri, 22°02'S, 68°07'W
chm	25	LA1306 (PI 379029)	*Rick et al. 390*	Fac-SC	Peru. Ayacucho: Tambo, 12°56'S, 74°01'W, 1 km E of Tambo, 3100 m
chm	27	LA1327	*Rick et al. 411*	Fac-SC	Peru. Apurímac: Soracata, 1980 m
chm	26	LA2663	*Rick et al. 6101*	Fac-SC	Peru. Cusco: Tujtohaiya (Upper Apurímac), 2500 m
lypc	5	LA1226 (PI 379045)	*Rick et al. 309*	Aut-SC	Ecuador. Morona-Santiago: 3 km S of Sucua, 1000 m
lypc	21	LA1673	*Rick et al. 1985*	Aut-SC	Peru. Lima: Ñaña, 11°59'S, 76°50'W, along W wall of the Estancia
hab	11	LA1353 (PI 365934)	*Rick et al. 437*	Allo-SI	Peru. Cajamarca: Contumazá, 2650 m, 7°22'S, 78°49'W
hab	24	LA1928	*Rick et al. 3170*	Fac-SC	Peru. Ica: Ocaña, Río Ingenio, 76 km from Panamerican Hwy., 2660 m, 14°39'S, 75°15'W
habg	3	LA1223 (PI 365903)	*Rick et al. 301*	Fac-SC	Ecuador. Chimborazo: Alausí, 2°12'S, 78°50'W, 2200 m
neo	7	LA2200	*Rick et al. 5045*	Aut-SC	Peru. Amazonas: Choipiaco, Río Suche, 6°13'S, 77°51'W, 16 km E of Chachapoyas, 1900 m
neo	17	LA247	*Ochoa 1017*	Aut-SC	Peru. Huánuco: Chavinillo, 9°47'S, 76°35'W

neo	20	LA1326 (PI 379033)	*Rick et al. 410*	Aut-SC	Peru. Apurímac: Río Pachachaca, 1980 m, 11°39′S, 76°01′W
pen	19	LA1376 (PI 379017)	*Rick et al. 460*	Allo-SI	Peru. Lima: Sayán, 1000 m, Agua Perdida (Río Ingenio), 11°06′S, 77°39′W
pen	31	LA716 (PI 246502)	Unknown	Fac-SC	Peru. Arequipa: Atico, near Atico from Chala along Panamerican Hwy., 16°14′S, 73°39′W
penp	28	LA1926	*Rick et al. 3168*	Allo-SI	Peru. Ica: 25 km from Panamerican Hwy., 1200 m, 14°38′S, 75°04′W
per	6	LA2185	*Rick et al. 5030*	Allo-SI	Peru. Amazonas: Pongo de Rentema, in the gap of the Marañón, E of Corral Quemado, 400 m, 5°26′S, 79°39′W
per	9	LA2172	*Rick et al. 5017*	Allo-SI; possibly SC or segregating SI/SC	Peru. Cajamarca: Cuyca, 161 km from Olmos junction with the Panamerican Hwy., 11°31′S, 75°07′W
per	9	LA2163	*Rick et al. 5008*	Allo-SI	Peru. Cajamarca: between Cochabamba and Yamaluc, 2–5 km N of Cochabamba, 1800–1900 m
per	9	LA2157	*Rick et al. 5002*	Fac-SC	Peru. Cajamarca: Tunel Chotano, 23 km N of Chota, 1600 m
per	11	LA392	*Rick et al. 141*	Allo-SI	Peru. Cajamarca: Llallan, 78 km from Car. Panamerican Hwy., 12 km W of Chile, 900 m
perh	11	LA2152	*Rick et al. 4997*	Allo-SI	Peru. Cajamarca: Río Jequetepeque, 140 km from Panamerican Hwy., 2 km W of San Juan, 2150 m, 7°17′S, 78°29′W
perh	11	LA2548	PE-29	Allo-SI	Peru. Cajamarca: La Muyuna, Río Jequetepeque, 870 m
per	10	LA1396	*Rick et al. 480*	Allo-SI	Peru. Amazonas: Balsas, 4°25′S, 80°17′W
per	13	LA2553	PE-31	Allo-SI	Peru. Cajamarca: Balconcillo-San Marcos, 2650 m, 7°20′S, 78°11′W
per	12	LA441	*Rick et al. 128*	Allo-SI	Peru. La Libertad: Cerro Campana, W of Panamerican Hwy. N of Trujillo, 350 m, 5°05′S, 79°17′W
per	12	LA1984	*Rick et al. 3225*	Allo-SI	Peru. La Libertad: Otuzco (Río Moche), 2 km on side road E of Otuzco, 2800 m, 7°54′S, 78°35′W
per	13	LA2328	*Rick et al. 5172*	Allo-SI	Peru. La Libertad: Aricapampa, 2300–2500 m, 7°48′S, 77°43′W
per	14	LA1982	*Rick et al. 3223*	Allo-SI	Peru. Ancash: Huallanca, Río Santa, near the hydroelectric plant, about 4 km beyond LA1981, 1400 m, 8°49′S, 77°52′W
per	15	LA1626	Unknown	Allo-SI	Peru. Ancash: mouth of Río Rupac, 1700 m
per	16	LA1360 (PI 365952)	*Rick et al. 444*	Allo-SI	Peru. Ancash: Pariacoto, 1490 m, 9°31′S, 77°53′W
per	18	LA111	*Rick et al. 41*	Allo-SI	Peru. Lima: Supe, along Panamerican Hwy. at km 158, 50 m, 10°48′S, 77°44′W
per	18	LA110	*Rick et al. 39*	Allo-SI	Peru. Ancash: Cajacay, 5 km W of Cajacay, 2500 m, 10°10′S, 77°26′W

TABLE 1 CONTINUED.

Taxon[a]	Map Locality[b]	Accession Number[c]	Collector[d]	Breeding System[e]	Locality[f]
per	18	LA1365 (PI 365953)	*Rick et al. 449*	Allo-SI	Peru. Ancash: Caranquilloc, 2450 m
per	19	LA1379 (PI 379018)	*Rick et al. 463*	Allo-SI	Peru. Lima: Caujul, 1500 m, 10°48′S, 77°02′W
per	21	LA1274 (PI 365940)	*Rick et al. 356*	Allo-SI	Peru. Lima: Pacaibamba, 1440 m
per	21	LA370	*Rick et al. 115*	Allo-SI	Peru. Lima: Huampani Quebrada, 200 m
perg	21	LA364	*Rick et al. 109*	Allo-SI	Peru. Lima: 9 km W of Canta, 2100 m, 12°35′S, 69°09′W
perg	21	LA1283 (PI 365942)	*Rick et al. 365*	Allo-SI	Peru. Lima: Santa Cruz de Laya, 2000 m
per	21	LA103	*Rick et al. 28*	Allo-SI	Peru. Lima: Cajamarquilla, on both sides of dry wash, 100 m, 6°25′S, 79°14′W
per	22	LA107	*Rick et al. 33*	Allo-SI	Peru. Lima: Hacienda San Isidro, 5°33′S, 80°49′W
per	23	LA1339 (PI 365949)	*Rick et al. 423*	Allo-SI	Peru. Lima: Capillucas, 1700 m, 13°39′S, 12°45′W
per	23	LA444	*Rick et al. 198*	Allo-SI	Peru. Ica: Chincha, southern outskirts, 100 m, 17°20′S, 71°00′W
per	24	LA1305 (PI 379015)	*Rick et al. 389*	Allo-SI	Peru. Huancavelica: 20 km E of Ticrapo, 2960 m
per	24	LA1910	*Rick et al. 3152*	Allo-SI	Peru. Huancavelica: Ticrapo, Tambillo (Río Ica), 74 km from Ica, 2300 m
per	28	LA1913	*Rick et al. 3155*	Allo-SI	Peru. Ica: Tinguiayog (Río Santa Cruz), 15 km from Panamerican Hwy., 900 m
per	28	LA1331 (PI 365946)	*Rick et al. 415*	Allo-SI	Peru. Ica: Nazca, 1500 m, 14°50′S, 74°57′W
per	29	LA1937	*Rick et al. 3179*	Allo-SI	Peru. Arequipa: Quebrada Torrecillas, (Río Chaparra), 21 km from Chaparra, 64 km from Panamerican Hwy., 2500 m, 15°55′S, 74°07′W
per	30	LA448	*Rick et al. 202*	Allo-SI	Peru. Arequipa: Chala, 15°52′S, 74°16′W
per	30	LA1945	*Rick et al. 3186*	Allo-SI	Peru. Arequipa: Caravelí, 71 km from Panamerican Hwy., 8 km before reaching Caravelí, 1940 m, 15°46′S, 73°22′W
per	32	LA1474	Unknown	Allo-SI	Peru. Arequipa: Lomas de Camaná, 1300 m, 16°22′S, 73°01′W
per	33	LA1973	Unknown	Allo-SI	Peru. Arequipa: Yura, 16°12′S, 71°42′W
per	35	LA3156	Unknown	Allo-SI	Peru. Moquegua: Omate Agricultural Valley
per	34	LA1954	*Rick et al. 3195*	Allo-SI	Peru. Arequipa: 2–4 km W of Mollendo, 50 m, 17°02′S, 72°01′W

per	34	LA454	*Rick et al. 208*	Allo-SI	Peru. Arequipa: 8 km S of Río Tambo crossing, 1200 m
per	36	LA2964	Unknown	Allo-SI	Peru. Tacna: Quebrada de Los Burros
per	37	LA2744	*Rick et al. 7502*	Allo-SI	Chile. Tarapaca: Sobraya, (Azapa), 31 km from Arica, 400 m
pim	2	LA1237 (PI 365910)	*Rick et al. 318*	Aut-SC	Ecuador. Esmeraldas: Atacames, 5 m
pim	8	LA1581	*Rick et al. 1861*	Fac-SC	Peru. Lambayeque: Punto Cuatro, 1 km W of Panamerican Hwy.
pim	23	LA1606	*Rick et al. 1886*	Aut-SC	Peru. Ica: Tambo de Mora, Huaucas, 13°28’S, 76°12’W
Outgroup, *Solanum* sect. *Lycopersicum* subsect. *Lycopersicoides* Child					
lyc	36	LA2386	*Ochoa 14248*	Allo-SI	Peru. Tacna: Chupapalca, 3180 m
sit	39	LA2876	*Rick et al. 7601*	Allo-SI	Chile. Antofagasta: Chuquicamata

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[a] Species abbreviations [and *Lycopersicon* synonyms] are:

chl = *S. chilense* (Dunal) Reiche [*Lycopersicon chilense* Dunal];

chm = *S. chmielewskii* (C. M. Rick, Kesicki, Fobes & M. Holle) D. M. Spooner, G. J. Anderson & R. K. Jansen [*L. chmielewskii* C. M. Rick, Kesicki, Fobes & M. Holle];

chs = *S. cheesmaniae* (L. Riley) Fosberg [*L. cheesmaniae* L. Riley];

gal = *S. galapagense* S. Darwin & Peralta [*L. cheesmaniae* f. *minor* (Hook. f.) C. H. Müll.] ;

hab = *S. habrochaites* S. Knapp & D. M. Spooner [*L. hirsutum* Dunal];

habg = *S. habrochaites* f. *glabratum* C. H. Müll.;

lyc = *S. lycopersicoides* Dunal [*L. lycopersicoides* (Dunal) A. Child ex J. M. H. Shaw];

lyp = *S. lycopersicum* L.;

lypc = *S. lycopersicum* L. var. *cerasiforme* (Dunal) D. M. Spooner, G. J. Anderson & R. K. Jansen [*L. esculentum* Mill. var. *cerasiforme* Dunal];

neo = *S. neorickii* D. M. Spooner, G. J. Anderson & R. K. Jansen [*L. parviflorum* C. M. Rick, Kesicki, Fobes & M. Holle];

pen = *S. pennellii* Correll [*L. pennellii* (Correll) D’Arcy];

penp = *S. pennellii* var. *puberulum* Correll;

per = *S. peruvianum* L. [*L. peruvianum* (L.) Miller];

perg = *L. peruvianum* f. *glandulosum* C. H. Müll.;

perh = *L. peruvianum* var. *humifusum* C. H. Müll.;

pim = *S. pimpinellifolium* L. [*L. pimpinellifolium* (L.) Miller];

sit = *S. sitiens* I. M. Johnst. [*L. sitiens* (I. M. Johnst.) J. M. H. Shaw];

[b] Map numbers correspond to Figure 1; G refers to unmapped accessions from the Galápagos Islands located about 1000 km west of Ecuador.

[c] LA numbers are from the C. M. Rick Tomato Genetics Resource Center; PI numbers are the same United States Plant Introduction Number duplicate accessions held at the United States Department of Agriculture genebank in Geneva, New York (Geneva Plant Genetic Resources Unit, NE-9).

[d] The collector abbreviation in the database of the C. M. Rick Tomato Genetics Resource Center is SAL, an abbreviation used by Rick for his collections alone or with others to indicate “South American *Lycopersicon*.”

[e] Allo = allogamous, Aut = autogamous, SC = self-compatible, SI = self-incompatible.

[f] Longitude and latitude data added by the authors.

unlikely, and only a few cases have been reported of spontaneous introgression between the two closely related *L. esculentum* and *L. pimpinellifolium* (Rick, 1986b).

In addition, Rick (1963, 1986b) recognized 40 informally designated races or ecotypes in the polymorphic *S. peruvianum*. A few of these are widespread coastal races, but the majority are locally distributed montane races. He proposed that strict gametophytic self-incompatibility and geographic isolation drove differentiation among the *S. peruvianum* races (Rick, 1986b). Hybridization showed an almost complete reproductive barrier between variety *humifusum*, a race growing at high altitude (2500 m) in the Jequetepeque River in northeast Peru, and most of the other *S. peruvianum* populations. Nevertheless, the reproductive isolation was not complete, due to the existence of some bridge races (races theoretically able to maintain gene flow between northern and southern races) located in central Peru (Rick, 1963, 1986b).

Studies of additional collections and crosses of northern populations of *Lycopersicon peruvianum* allowed Rick (1986b) to identify four groups of races that were isolated by reproductive barriers. Three groups of races occur in northern Peru: the Chamaya-Cuvita group of races, the Marañón group of races, and Chotano-*humifusum* group of races. The fourth group of races comprised all the remaining races of *L. peruvianum* from central and southern Peru. Rick (1986b) confirmed the crossing barriers between the northern and southern races, and found that some of the northern races crossed to a limited degree with *L. chilense*, *L. hirsutum*, and *L. esculentum*. Based on these findings, Rick (1986b) hypothesized that the Río Marañón races of *L. peruvianum* were ancestral to all other wild tomatoes.

The Endosperm Balance Number (EBN) crossability phenomenon was analyzed for Rick's two wild tomato complexes by Ehlenfeldt and Hanneman (1992). The EBN hypothesis (Johnston et al., 1980; Ortiz & Ehlenfeldt, 1992; Hanneman, 1994) postulates that in the absence of stylar barriers, the success or failure of a cross is determined primarily by a 2:1 maternal to paternal balance in the endosperm, independent of ploidy. The EBN is determined using standard crossing species with known EBNs. The EBN data supported the hypothesis of two intra-fertile groups as proposed by Rick (1979). The Esculentum complex showed uniformity of EBN values, which can be compared to the 2x(1EBN) species in potato. On the other hand, the Peruvianum complex showed variable values for EBN, but most comparable to 2x(2EBN) potato species (Ehlenfeldt & Hanneman, 1992). These authors hypothesized that the Esculentum and Peruvianum complexes are separated by a system analogous to the 2x(1EBN) *S. commersonii* and 2x(2EBN) *S. chacoense* crossability groups. This isolating mechanism may restrict or suppress gene flow among sympatric populations, and may play a role in the reproductive isolation in tomatoes like in the *L. peruvianum* var. *humifusum* races from northern Peru (Ehlenfeldt & Hanneman, 1992).

Molecular data from chloroplast DNA restriction site and sequence data (Spooner et al., 1993; Bohs & Olmstead, 1997, 1999; Olmstead & Palmer, 1997; Olmstead et al., 1999) firmly place tomatoes and potatoes as sister taxa. The systematic placement of tomatoes under *Solanum*, as adopted here, is beginning to gain acceptance in the taxonomic literature (Bohs & Olmstead, 1997, 1999; Olmstead & Palmer, 1997), but it is still controversial and highlights competing goals and hypotheses of classification (Peralta & Spooner, 2000).

Peralta and Spooner (2001) examined interspecific relationships of all 10 wild tomato species, with a concentration on the highly polymorphic and widespread species *Solanum peruvianum*, with DNA sequence data of the single-copy nuclear encoded GBSSI gene. Their outgroup results were concordant with the cpDNA restriction fragment length polymorphism (RFLP) phylogeny of Spooner et al. (1993), supporting *S. juglandifolium*, *S. lycopersicoides*, and *S. sitiens* as outgroups. The ingroup of wild tomatoes showed a basal polytomy and a terminal clade. The basal polytomy was composed of the self-incompatible green-fruited species *S. chilense*, the central to southern Peruvian populations of *S. peruvianum*, *S. habrochaites*, and *S. pennellii*. The terminal clade contained the northern Peruvian populations of *S. peruvianum* (also self-incompatible, green fruits), *S. chmielewskii*, and *S. neorickii* (self-compatible, green fruits), and the self-compatible and red- to orange- to yellow-fruited species *S. cheesmaniae, S. galapagense, S. lycopersicum*, and *S. pimpinellifolium* (Fig. 2). The results supported allogamy, self-incompatibility, and green fruits as plesiomorphic in tomatoes.

We wished to examine morphology as an independent and taxonomically accessible data set, using the same accessions in the GBSSI study (Peralta & Spooner, 2001). All prior classifications used morphology for intuitive taxonomic judgments, and this is the first explicit use of morphology for phenetic and cladistic analyses in tomatoes. The goals of this study are: (1) to examine interrelationships among all 10 wild tomato species with phenetic and cladistic analyses of morphological data, and (2) to compare our results with the morphological (Müller, 1940; Luckwill, 1943) and biological (Rick, 1979; Rick et al., 1990) classifications; mitochondrial DNA restriction site results (McClean & Hanson, 1986); nuclear DNA RFLP results (Miller & Tanksley, 1990), cpDNA restriction site results of Palmer and Zamir (1982) and Spooner et al. (1993), and GBSSI DNA sequence results (Peralta & Spooner, 2001). Our results show diagnostic characters useful for species differentiation for a monographic study of *Solanum* sect. *Lycopersicon*, currently in progress.

MATERIALS AND METHODS

SPECIES

For phenetic analyses, we analyzed a total of 66 accessions of all 10 species of tomatoes (Table 1), including two species of *Solanum* subsect. *Lycopersicoides* supported as a close outgroup of tomato (Rick, 1979, 1988; Child, 1990; Spooner et al., 1993). All the accessions, representing much of the ingroup variation, were obtained from the C. M. Rick Tomato Genetics Resource Center, Department of Vegetable Crops, University of California, Davis. The late Charles Rick, former curator of this gene bank, kindly provided advice on the choice of accessions, based on geographic distribution, morphology, genetic diversity, and breeding behavior (Fig. 3; Table 1). He also advised us on critical morphological characters to differentiate taxa (Table 2). The accessions represent nearly the same as those used in the GBSSI gene phylogenetic analysis of Peralta and Spooner (2001).

Three accessions per species were analyzed for *Solanum chmielewskii*, *S. chilense*, *S. habrochaites*, *S. neorickii*, *S. pennellii*, *S. pimpinellifolium*, two accessions for *S. lycopersicum* var. *cerasiforme* and *S. cheesmaniae*, one accession of *S. galapagense*, and 41 accessions for *S. peruvianum*. One accession of *S. lycopersicoides* and one accession of *S. sitiens* were included as closely related non-tomato comparison species. For cladistic analyses, we determined taxon-specific characters (Tables 3, 4) based on results from the character state variation and phenetic analyses.

The plants were grown in the fall, because some wild tomato species need short photoperiods to flower. Seeds were planted in greenhouses of the University of Wisconsin, Madison, in mid August 1999. Two weeks later, seedlings were transferred to 30 cm diameter plastic pots with sterilized soil. Three plants per accession were randomly distributed in two replicates, and a total of six individuals were evaluated per accession. Stem characters and leaves were measured from the ninth node, when plants developed more than 12 nodes and were usually between 60 and 80 cm high. Most of the plants began to flower by the end of September or the first week of October. Flowers were collected from mature inflorescences when the plants were in full bloom, during the months of October, November, and December. In order to

TABLE 2.

Morphological characters used in the phenetic analysis of wild tomatoes and outgroups. All measurements are in millimeters, except as noted below. Characters marked with an asterisk (*) were not significantly different (*P* = 0.05) between at least two species under the Tukey-Kramer HSD test.

STEM CHARACTERS

1. Stem diameter at base. 2. Internode length between the 9th and 10th node (cm). 3. Number of branches in the first 20 cm at flowering time. 4. Number of nodes before branch bifurcation. 5. Plant height at branch bifurcation (cm). 6. Pseudostipules: absent (0); present (1). 7. Number of leaves per sympodium.

LEAF CHARACTERS

8. Leaf length (cm). 9. Ratio: leaf length/leaf width. 10. Ratio: leaf length/length of leaf from widest point to leaf apex. 11. Leaf petiole length (cm). 12. Terminal leaflet lamina length (cm)*. 13. Ratio: length of terminal leaflet lamina/width of lamina. 14. Ratio: length of terminal leaflet lamina/length of terminal leaflet lamina from its widest point to apex. 15. Terminal leaflet petiolule length (cm)*. 16. Width of terminal leaflet lamina from a point 5 mm below the apex (cm). 17. Length of primary dorsal leaflet lamina (cm). 18. Ratio: length of primary dorsal leaflet lamina/width of lamina. 19. Ratio: length of primary dorsal leaflet lamina/length of primary dorsal leaflet lamina from its widest point to apex. 20. Length of primary dorsal leaflet petiolule. 21. Width of primary dorsal lateral leaflet lamina from a point 5 mm below the apex. 22. Number of lateral leaflets. 23. Number of interjected leaflets. 24. Number of secondary leaflets. 25. Number of tertiary leaflets.

INFLORESCENCE CHARACTERS

26. Inflorescence bracts: absent (0); present (1). 27. Number of branches per mature inflorescence. 28. Number of flowers per branch*. 29. Length of the mature inflorescence axis (cm). 30. Ratio: number of flowers/length of inflorescence axis. 31. Peduncle length (cm). 32. Ratio: total inflorescence length/peduncle length.

FLOWER CHARACTERS

33. Pedicel length (cm). 34. Ratio: pedicel length from base of the pedicel to articulation/pedicel length. 35. Sepal length. 36. Ratio: sepal length/width. 37. Length from center of corolla to apex of corolla lobe (cm). 38. Ratio: length from center of corolla to apex of corolla lobe/length from center of corolla to base of corolla lobe. 39. Width of corolla lobe at base of corolla lobe junction (cm)*. 40. Ratio: length from a line drawn across the widest point of corolla lobe to lobe apex/width of corolla lobe at base of corolla lobes junction. 41. Anther length. 42. Anther appendage length. 43. Anther filament length. 44. Anther appendage curvature: straight (1), slightly curved to 40° (2), curved more than 45° (3). 45. Anther attachment: free (0), attached (1). 46. Anther dehiscence: pores (0), longitudinal split (1). 47. Anther color: white (0), yellow (1). 48. Style length exsertion from apex of anthers to stigma apex. 49. Stigma width. 50. Ovary length. 51. Style length (cm).

FRUIT CHARACTERS

52. Diameter at its widest dimension. 53. Ratio: diameter at widest dimension/diameter at narrowest dimension*. 54. Ratio: diameter at widest dimension/fruit length. 55. Fruit color: green (1), pale green (2), yellow green (3), orange (4), red (5). 56. Fruit stripe: absent (0); present (1). 57. Fruit pubescence: glabrous to glabrescent (1), pubescent to pilose (2), hirsute (3).

PLANT TRICHOMES

See Luckwill (1943) for illustrations of trichome types, and materials and methods for the method of scoring.

58. Type I. 59. Type II. 60. Type III. 61. Type IV. 62. Type V. 63. Type VI. 64. Type VII*. 65. Type VIII*. 66. Trichome density.

obtain fruits from the self-incompatible (SI) accessions, plants were pollinated manually using pollen of different individuals belonging to the same accessions. Self-compatible (SC) accessions produced fruits naturally. Fruits were harvested approximately two months after pollination. Vouchers are deposited at DAV, MERL, PTIS, and WIS.

DATA MEASUREMENT

For phenetic analyses, we assessed a total of 66 characters (50 quantitative and 16 qualitative) for 6 individuals of 66 accessions (over 26,000 data points). The quantitative characters included 14 ratios that assessed shapes of different plant organs (Table 2). Trichomes were studied from young stems by making thin slice cuts 1 or 2 cm below the apex with a razor blade. Trichome types were identified according to the classification of Luckwill (1943) using a transmission light microscope (100× magnification). An arbitrary scale based on percentages: 1%–20% = 1, 21%–40% = 2, 41%–60% = 3, 61%–80% = 4, 81%–100% = 5, was used to score the frequency of different trichomes (characters 58 to 65). The diameter and height of the thin stem slice were measured under a microscope, and the number of trichomes around the slice circumference was counted. Trichome density percentage (D = n/S 100; character 66) was estimated as the total number of trichomes (n) divided by the cylinder square ($S = \pi \times \text{diameter}/2 \times \text{height}$), represented by the thin stem slide.

For cladistic analyses, we chose characters that were shown by our analysis of character state variation (below) to have non-overlapping or nearly non-overlapping states (Table 3).

DATA ANALYSIS: CHARACTER STATE VARIATION AND PHENETICS

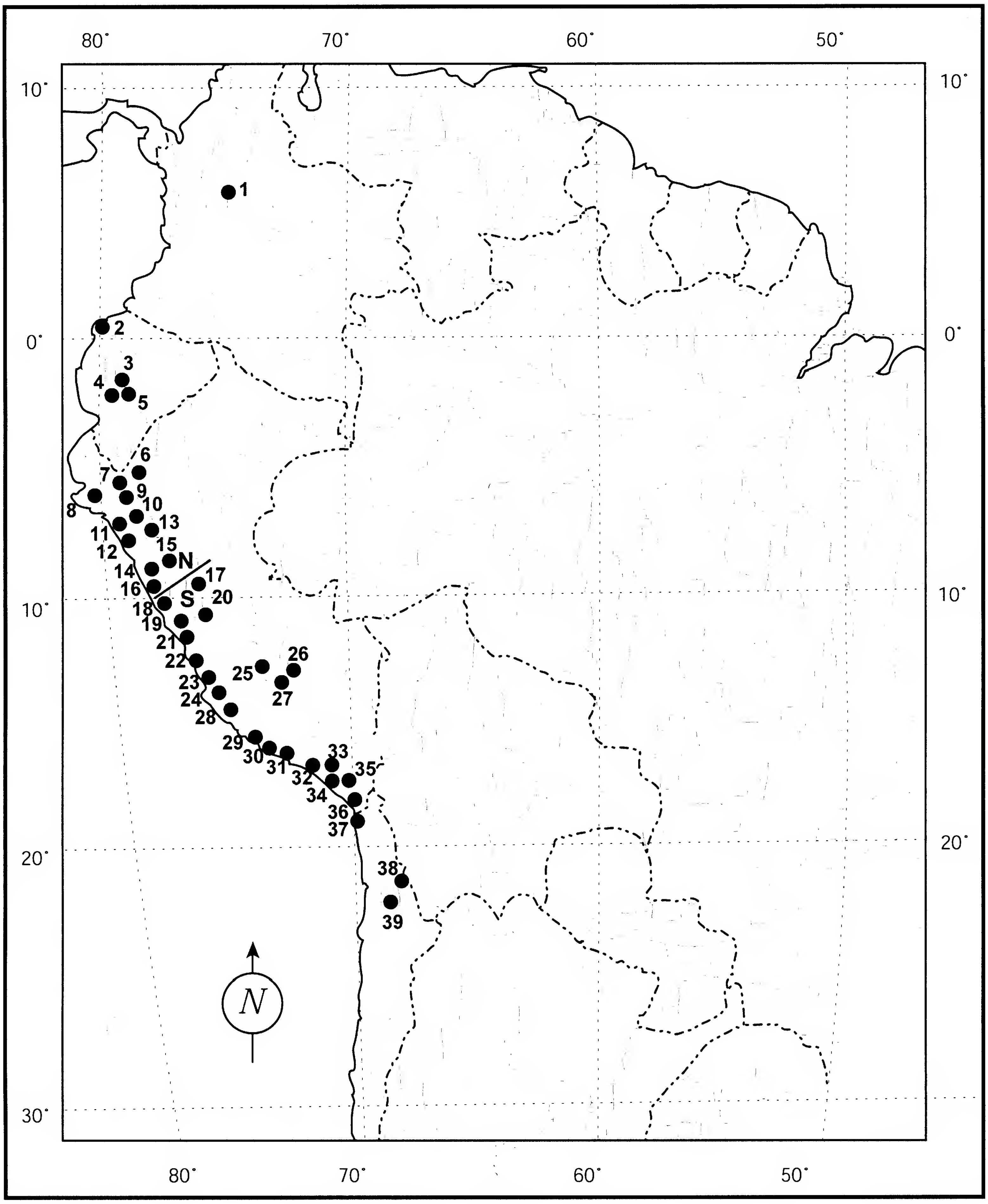
The mean value of the six plants per accession was used as the Operational Taxonomic Unit (OTU). The mean, range, and standard deviation were estimated for each character. Significant character state differences ($P = 0.05$) between any two pairs of species were evaluated using the Tukey-Kramer test with JMP statistical software (SAS, 1995).

Cluster analyses were produced by NTSYS-pc^R version 1.70 (Rohlf, 1992) only on the subset of 66 characters found to be statistically significant among groups by one-way ANOVA. Averages for each character were standardized (STAND), and similarity matrices, using average taxonomic distance (DIST), Manhattan distance (MANHAT), Euclidean distance (EUCLID), and product-moment correlation (CORR) were generated. Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN. Cophenetic correlation coefficients (COPH and MXCOMP) were used to measure distortion between the similarity matrices and the resultant three phenograms (Rohlf & Sokal, 1981; Sokal, 1986). Stepwise discriminant analysis (SDA) was performed on all 66 characters by SAS Version 7 (SAS, 1998), using the mean values.

Four entities in *Solanum peruvianum* (the northern and southern populations, f. *glandulosum,* and var. *humifusum*), *S. cheesmaniae,* and *S. galapagense* (= *S. cheesmaniae* f. *minor*), were recognized as OTUs to estimate the mean, range, and standard deviation. In addition to these taxa, two forms of *S. habrochaites* (f. *typicum* and f. *glabratum*) and two varieties of *S. pennellii* (var. *typicum* and var. *puberulum*) were considered in the cluster analysis and in the SDA. The forms and varieties of the latter two species are mainly differentiated by their pubescence.

DATA ANALYSIS: CLADISTICS

We used two subsets of characters that represented all (26 characters, data set 1), or only those characters lacking division into ranges of states (15 characters, data set 2) (Tables 3, 4). Parsimony analyses were conducted with PAUP* 4.0d64 (Swofford, 1998). *Solanum juglandifolium*, *S. lycopersicoides*, *S. ochranthum*, and *S. sitiens* were used as outgroups based on Rick


80°
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S
N

Figure 3. Distribution of the wild tomato accessions used in this study. Map numbers correspond to generalized map localities in Table 1. The line indicates the geographic distribution of *S. peruvianum* north (N) and south (S).

TABLE 3.

Morphological characters used in cladistic analyses of wild tomatoes and outgroups. All 26 characters are used in data set 1; those marked with an asterisk (*) are eliminated for data set 2 containing 15 characters. Consistency Index (CI) and Retention Index (RI) were estimated for each character. The RI is not applicable (n.a.) for autapomorphic characters.

1.* Number of nodes before branch bifurcation: 1, > 30; 2, 17–20; 3, 10–15; 4, < 10. CI = 1, RI = 1.
2. Number of leaves per sympodium: 1, > 5; 2, 3; 3, 2. CI = 0.667, RI = 0.857.
3. Pseudostipular leaves: 1, absent; 2, present. CI = 1, RI = 1.
4.* Number of lateral leaflet pairs: 1, 4–5; 2, 2–4. CI = 0.5, RI = 0.5.
5.* Number of secondary leaflets: 1, 0–5; 2, 5–10; 3, 10–20; 4, 40–50. CI = 1, RI = 1.
6. Tertiary leaflets: 1, absent; 2, present. CI = 1, RI = n.a.
7.* Leaflet width 5 mm below the apex: 1, > 15 mm; 2, < 10 mm. CI = 1, RI = n.a.
8.* Inflorescence peduncle length: 1, > 7 cm; 2, 5–7 cm; 3, 3–5; 4, < 3 cm. CI = 0.750, RI = 0.833.
9.* Branches per inflorescence: 1, > 4; 2, 2 often 3; 3, 1–2; 4, 1. CI = 1, RI = 1.
10. Bracts in inflorescence: 1, absent; 2, present. CI = 0.5, RI = 0.8.
11. Anthoclades (see Spooner et al., 1993): 1, 3.7; 2, 3.6. CI = 1, RI = 1.
12.* Pedicel articulation: 1, mid to upper position; 2, variable; 3, basal. CI = 1, RI = 1.
13. Corolla shape: 1, symmetrical; 2, asymmetrical. CI = 1, RI = n.a.
14.* Length from center of corolla to apex of corolla lobe: 1, > 1.5 cm; 2, 1–1.5 cm; 3, < 1 cm. CI = 0.667, RI = 0.667.
15. Anther color: 1, white; 2, yellow. CI = 1, RI = 1.
16. Anther lateral interlocking papillae: 1, absent; 2, small; 3, elongate. CI = 1, RI = 1.
17. Anther connation: 1, separate; 2, free but holding together; 3, tightly connate. CI = 1, RI = 1.
18. Anther appendages: 1, absent; 2, present. CI = 1, RI = 1.
19. Anther tube: 1, straight; 2, anther and appendages curved; 3, anther curved. CI = 1, RI = n.a.
20.* Style exsertion: 1, > 1.8; 2, 1–1.8; 3, 0.5–1; 4, 0.5–0. CI = 0.750, RI = 0.857.
21. Fruit color: 1, green; 2, yellow to orange; 3, red. CI = 1, RI = 1.
22.* Fruit size: 1, > 25 mm diam. at widest point; 2, 15–25 mm diam. at widest point; 3, 5–15 mm diam. at widest point; 4, < 5 mm diam. at widest point. CI = 1, RI = 1.
23. Fruit pericarp: 1, thick and hard pericarp; 2, thin and leathery; 3, thin and membranaceous. CI = 1, RI = 1.
24. * Seeds: 1, more than 3 mm; 2, less than 3 mm. CI = 1, RI = 1.
25. Compatibility: 1, self-incompatible; 2, self-compatible. CI = 1, RI = 1.
26. Breeding: 1, allogamous; 2, autogamous/facultative allogamous; 3, autogamous. CI = 0.667, RI = 0.750.

TABLE 4. Data matrix of cladistic character states corresponding to Table 3.

		Characters and Character States																									
	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
OUTGROUPS	*Solanum lycopersicoides*	1	1	2	1	1	1	2	1	1	2	1	1	1	2	1	1	1	1	1	1	1	3	2	1	1	1
	S. sitiens	?	1	2	1	1	1	2	1	1	2	1	1	1	2	1	1	1	1	1	1	1	3	2	1	1	1
	S. ochranthum	1	1	2	2	1	1	2	2	1	1	2	2	1	2	2	2	2	1	1	1	1	1	1	1	1	1
	S. juglandifolium	1	1	2	2	1	1	2	2	1	1	2	2	1	2	2	2	2	1	1	1	1	1	1	1	1	1
INGROUPS	*S. pennellii*	3	3	2	2	1	1	1	2	3	2	1	3	2	1	2	2	3	1	3	1	1	3	3	2	1	1
	S. habrochaites	2	2	2	2	1	1	2	3	3	2	1	1	1	1	2	3	3	2	1	2	1	3	3	2	1	1
	S. chilense	3	3	2	1	1	1	2	1	2	2	1	1	1	1	2	3	3	2	1	2	1	3	3	2	1	1
	S. peruvianum south	3	3	2	2	1	1	2	2	2	2	1	1	1	1	2	3	3	2	2	2	1	3	3	2	1	1
	S. peruvianum north	3	3	2	2	1	1	2	2	4	2	1	1	1	2	2	3	3	2	1	3	1	3	3	2	1	1
	S. chmielewskii	3	3	2	2	1	1	2	4	4	2	1	1	1	2	2	3	3	2	1	3	1	3	3	2	2	2
	S. neorickii	3	3	2	2	1	1	2	4	4	2	1	1	1	3	2	3	3	2	1	4	1	3	3	2	2	3
	S. cheesmaniae	4	2	1	2	2	1	2	4	4	1	1	1	1	2	2	3	3	2	1	4	2	3	3	2	2	3
	S. galapagense	3	2	1	2	4	2	2	4	4	1	1	1	1	2	2	3	3	2	1	4	2	4	3	2	2	3
	S. pimpinellifolium	3	2	1	2	2	1	2	4	4	1	1	1	1	2	2	3	3	2	1	3	3	3	3	2	2	2
	S. lycopersicum	3	2	1	2	3	1	2	4	4	1	1	1	1	2	2	3	3	2	1	4	3	2	3	2	2	2

(1979, 1988), Child (1990), Spooner et al. (1993), and Peralta and Spooner (2001). *Solanum juglandifolium* and *S. ochranthum* are supported by GBSSI results as the sister taxa to tomatoes, but were not included in the phenetic analysis due to their slow growth in the greenhouse. We obtained flower, fruit, and seed cladistic characters of these species from the literature or from herbarium specimens.

Cladistic analyses were performed on both data sets 1 and 2, using Wagner parsimony, unordered character states, and all characters were equally weighted. The heuristic searches were performed using branch and bound and furthest addition sequence. The amount of homoplasy for both trees and individual characters was evaluated with the consistency index (CI) of Kluge and Farris (1969) and the retention index (RI) of Farris (1989). Consensus trees were generated from all most parsimonious trees. Bootstrap (Felsenstein, 1985) and Jackknife analyses, using 1000 replicates (using tree bisection reconnection and saving all multiple trees), were conducted to estimate the internal relative support for each branch.

RESULTS

CHARACTER STATE VARIATION

The Tukey-Kramer HSD test determined that 61 of the 66 characters were significantly different between at least two taxa (Table 2). The means, ranges, and standard deviations of the 30 characters showing most variation among species are presented in Figure 4. Separately, distribution of character states of "northern" and "southern" populations of *S. peruvianum*, chosen on the basis of the GBSSI results (Peralta & Spooner, 2001), were also compared using the Tukey-Kramer HSD test. Thirty-one characters were significantly different between these two groups of *S. peruvianum*. The means, ranges, and standard deviations of the 18 most important characters separating these geographic groups of *S. peruvianum* are illustrated in Figure 5.

PHENETIC RESULTS

The same dendrogram was produced by DIST (Fig. 6) and EUCLID, both with a cophenetic correlation coefficient of 0.93, which was only slightly higher than those produced by MANHAT, 0.91; CORR was 0.75. Cophenetic correlations between 0.8 and 0.9 can be interpreted subjectively as good fits to the cluster analysis, and those between 0.7 and 0.8 as poor fits (Rohlf, 1992).

The DIST phenogram has four main groups (Fig. 6A–D). The outgroups, *S. lycopersicoides* and *S. sitiens*, were clustered as the external branch (group D), followed by *S. galapagense*, and then a group of all three accessions of *S. pennellii* (group C). The self-compatible, red- to orange- to yellow-fruited species (*S. lycopersicum*, *S. cheesmaniae*, and *S. pimpinellifolium*) formed a third cluster (group A), but with the exclusion of the distinctive *S. galapagense*. The fourth group (B) included the remaining species.

Within group B, *Solanum neorickii* and two accessions of *S. chmielewskii* clustered together, to the exclusion of one accession of *S. chmielewskii* (LA 1306) that grouped with *S. peruvianum*. All accessions of *S. chilense* formed a group that also contained one accession of *S. peruvianum* (LA 1982). The three accessions of *S. habrochaites* formed a separate group. Concordant with the GBSSI sequence data, two major groups were recognized within *S. peruvianum*: "the northern" and "the southern" (Fig. 6 N, S). Only three *S. peruvianum* accessions were placed outside the northern and southern clusters (LA 2172, LA 1379, LA 1982).

We also present the CORR phenogram (Fig. 7) despite a lower cophenetic correlation (0.75; vs. DIST, 0.93), because it provides better phenetic support for *S. cheesmaniae* and *S. galapagense*, and north and south populations of *S. peruvianum*. Unlike the DIST phenogram, it places the two outgroups, *S. lycopersicoides* and *S. sitiens*, as an internal branch with one of two main clusters (A). The self-compatible, red- to orange- to yellow-fruited species: *S. cheesmaniae*, *S. galapagense, S. lycopersicum*, and *S. pimpinellifolium* grouped together within the cluster A. The three accessions of *S. habrochaites* formed a separate group, and also the three *S. pennellii* accessions clustered together. The other main branch (B) includes *S. peruvianum*, *S. chilense*, *S. neorickii*, and *S. chmielewskii*. The CORR phenogram, unlike the DIST phenogram, showed a better clustering of the northern and southern *S. peruvianum* groups (Fig. 7), and maintained all accessions of *S. cheesmaniae* and *S. galapagense* together. Like the DIST phenogram, *S. peruvianum* (LA 1982) clustered with *S. chilense*. The two accessions of *S. peruvianum* f. *glandulosum* clustered with the southern *S. peruvianum*. *Solanum neorickii*, *S. chmielewskii*, and the two accessions of *S. peruvianum* var. *humifusum* clustered with the northern *S. peruvianum*.

The SDA of all taxa discriminated 30 characters. The 10 best characters, in decreasing order of discriminative utility, were: (1) anther attachment, (2) anther color, (3) pseudostipules, (4) number of nodes, (5) number of tertiary leaflets, (6) number of leaves per symposia, (7) trichome type III, (8) anther length, (9) plant height, and (10) number of secondary leaflets.

The SDA of the northern and southern populations of *S. peruvianum* discriminated 11 characters, (1) number of inflorescence branches, (2) style exsertion, (3) dorsal leaflet petiolule, (4) fruit color, (5) ratio: articulation length/pedicel length, (6) anther curvature, (7) internode length, (8) trichome type V, (9) pedicel length, (10) trichome type IV, and (11) terminal leaflet length.

CLADISTIC RESULTS

The analysis using all 26 characters (Tables 3, 4) produced 28 equally parsimonious trees, length 54 (Fig. 8). The strict consensus tree (Fig. 9) has a CI = 0.870, Consistency Index excluding uninformative characters (CIU) = 0.857, and RI = 0.900. Bootstrap analysis using 10,000 replicates gave 96% support for the ingroup. Jackknife values (10,000 replicates) were similar or sometimes lower, but also support these groups (Fig. 9). In the ingroup *Solanum pennellii* is supported as basal. The relationships among the self-incompatible species *S. chilense*, *S. habrochaites*, and *S. peruvianum* south were not resolved, and the three taxa formed a polytomy in all 28 equally parsimonious trees (Fig. 9). *Solanum peruvianum* north appeared as basal to *S. chmielewskii* and *S. neorickii* (Fig. 9) in the 28 equally parsimonious trees with 76(64)% bootstrap (jackknife) support. *Solanum chmielewskii* and *S. neorickii* appeared always together and supported in a basal position in the same clade as the monophyletic group formed by *S. cheesmaniae*, *S. galapagense*, *S. pimpinellifolium*, and *S. lycopersicum* (Fig. 9).

When the breeding characters (Table 3: 25, 26) were excluded, 24 trees were obtained (length = 50; CI = 0.880, CIU = 0867, RI = 0.902). A strict consensus tree of these 24 trees is identical to the strict consensus tree using all 26 characters (Fig. 9). The analysis using the subset of 15 characters (Table 3) produced 10 equally parsimonious trees, length 26. The strict consensus tree (CI = 0.846, CIU = 0.818, RI = 0.895) is topologically the same that was obtained using all 26 characters (Fig. 9), except *S. peruvianum* north is now part of the polytomy with *Solanum chilense*, *S. habrochaites*, and *S. peruvianum* south.

CONCORDANT MORPHOLOGICAL CLADISTIC RESULTS

The cladistic results showed the following patterns of relationships: (1) Within the four outgroup taxa, *Solanum ochranthum* and *S. juglandifolium* were sister taxa and *S. lycopersicoides* and *S. sitiens* were sister taxa. (2) Within the tomato ingroup, *S. pennellii* was basal. (3) *Solanum cheesmaniae, S. galapagense*, *S. pimpinellifolium*, and *S. lycopersicum* were terminal taxa and monophyletic. (4) *Solanum chmielewskii* and *S. neorickii* appeared always together in a basal position in the same clade as *S. cheesmaniae*, *S. galapagense, S. pimpinelli-*

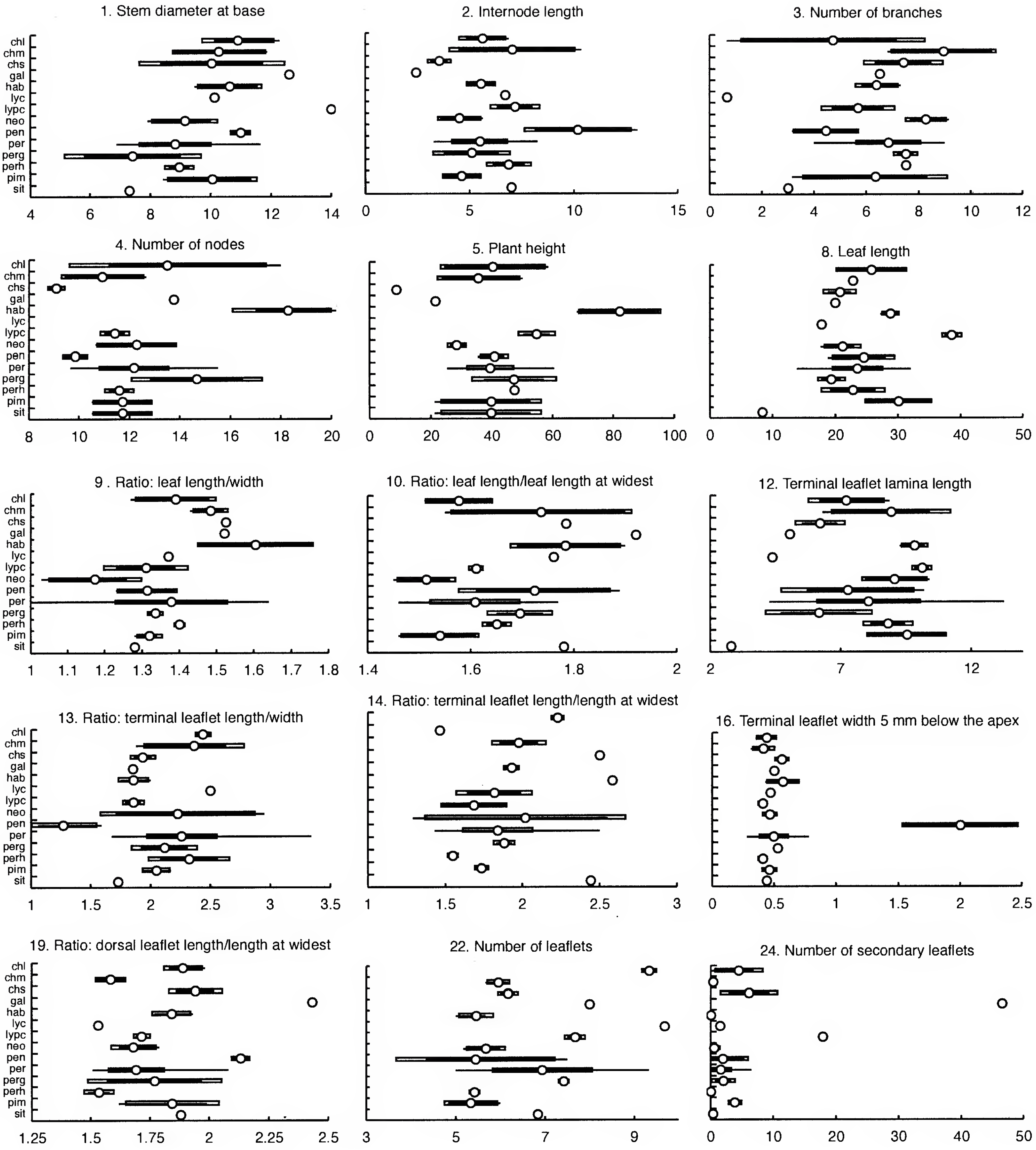

Figure 4. Means, ranges, and one standard deviation of the mean for the 30 of 66 characters examined in this study showing the greatest differences among taxa of *Solanum chilense* = chl; *S. chmielewskii* = chm; *S. cheesmaniae* = chs; *S. galapagense* = gal [= *S. cheesmaniae* f. *minor*]; *S. habrochaites* = hab; *S. lycopersicoides* = lyc; *S. lycopersicum* var. *cerasiforme* = lypc; *S. neorickii* = neo; *S. pennellii* = pen; *S. peruvianum* = per; *S. peruvianum* f. *glandulosum* = perg; *S. peruvianum* var. *humisufum* = perh; *S. pimpinellifolium* = pim; *S. sitiens* = sit.

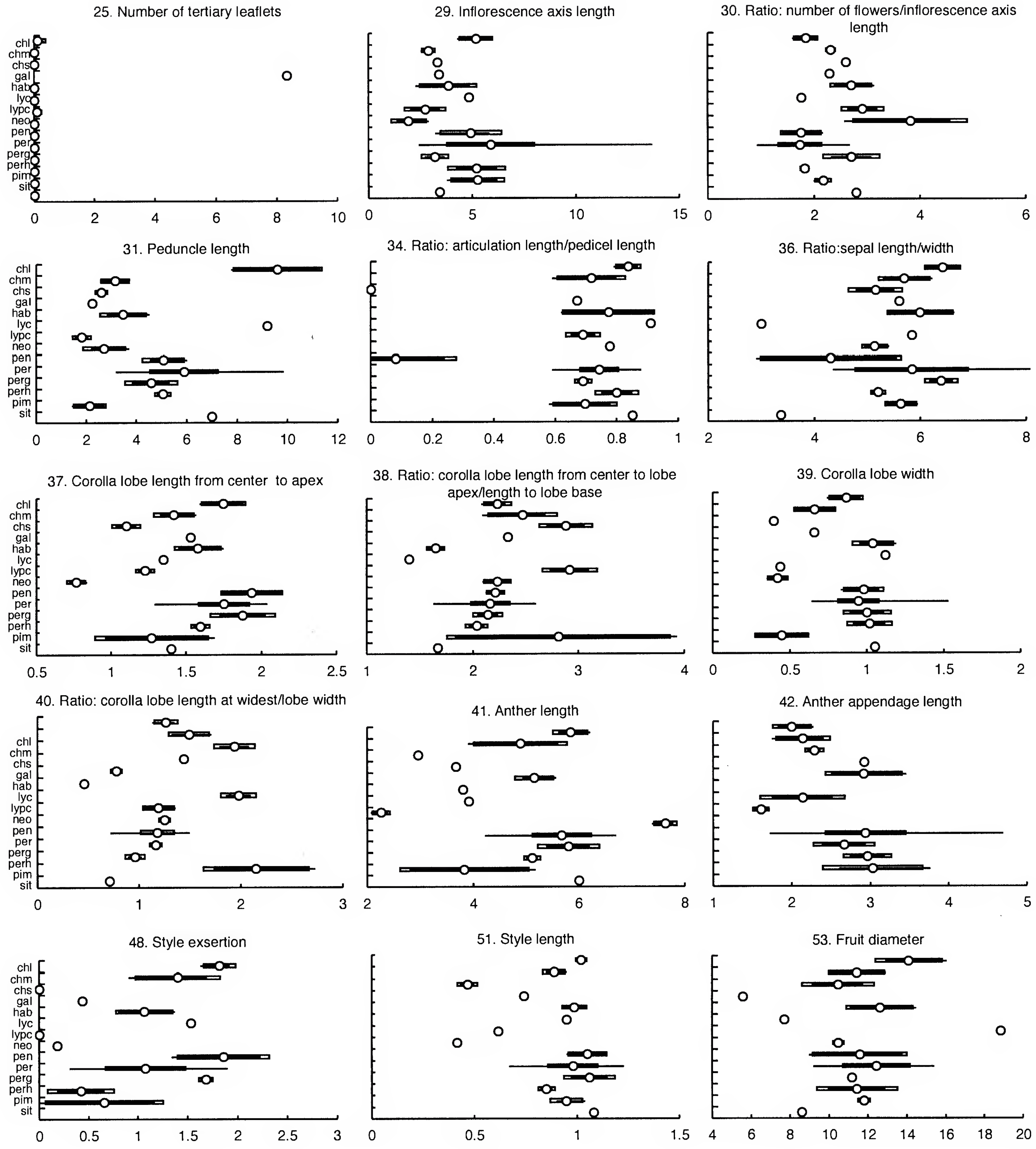

Figure 4 continued.

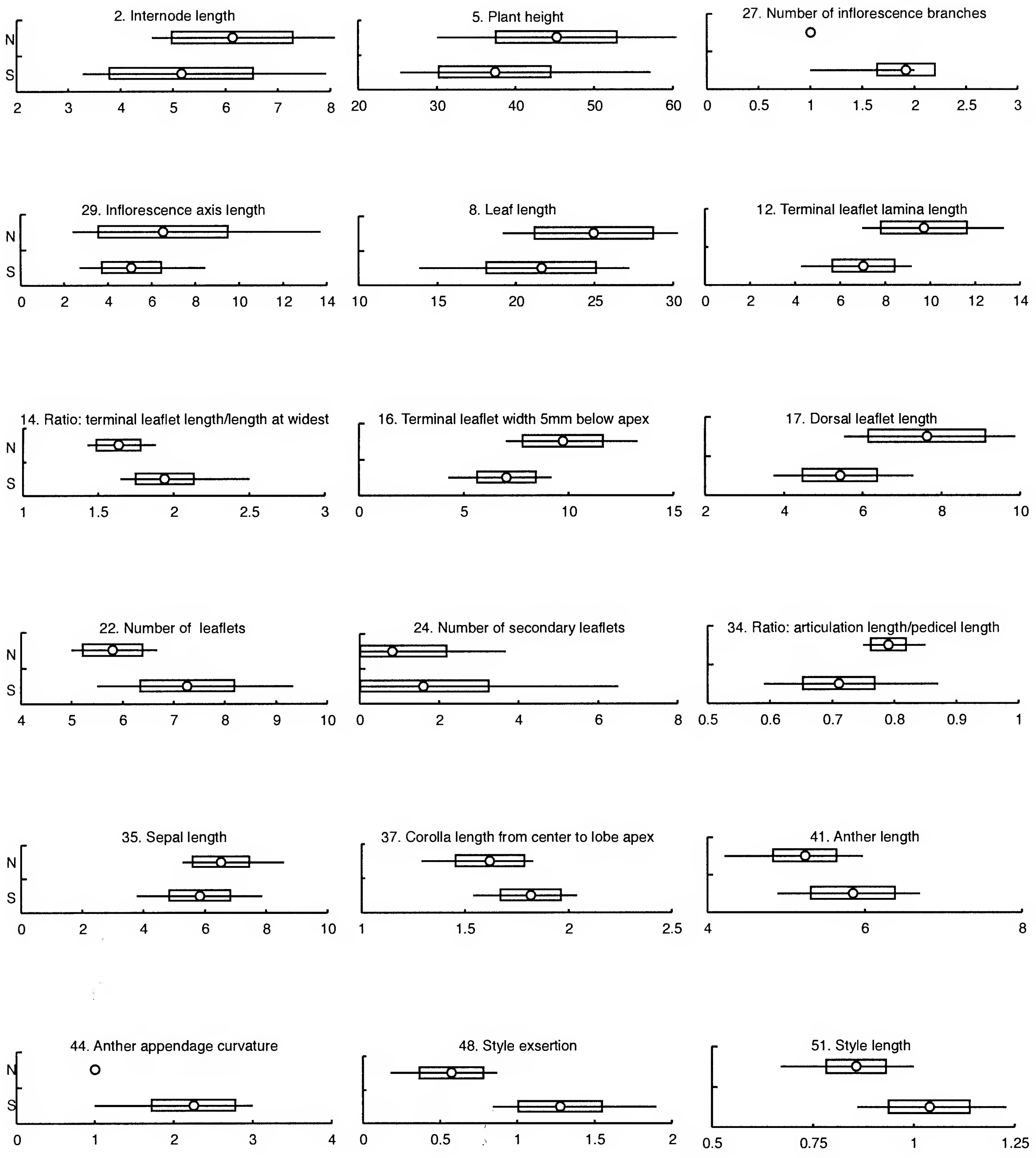

Figure 5. Means, ranges, and one standard deviation of the mean for the 18 of 61 characters examined in this study showing the greatest differences among *S. peruvianum* accessions from northern Peru = N, and southern Peru = S.

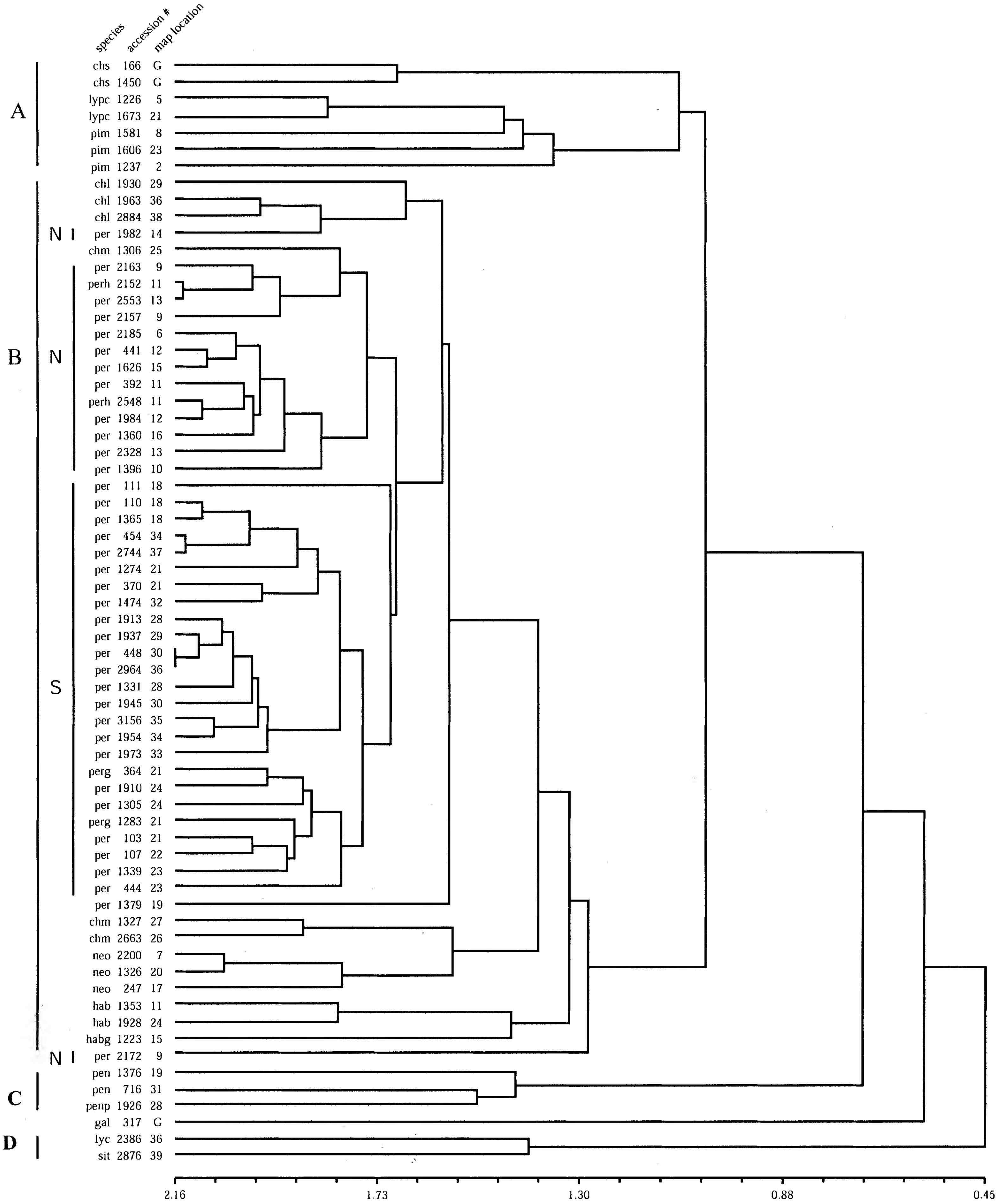

Figure 6. UPGMA dendrogram (DIST similarity option) based on 61 morphological characters. Species codes, accession numbers, and map locations as in Table 1.

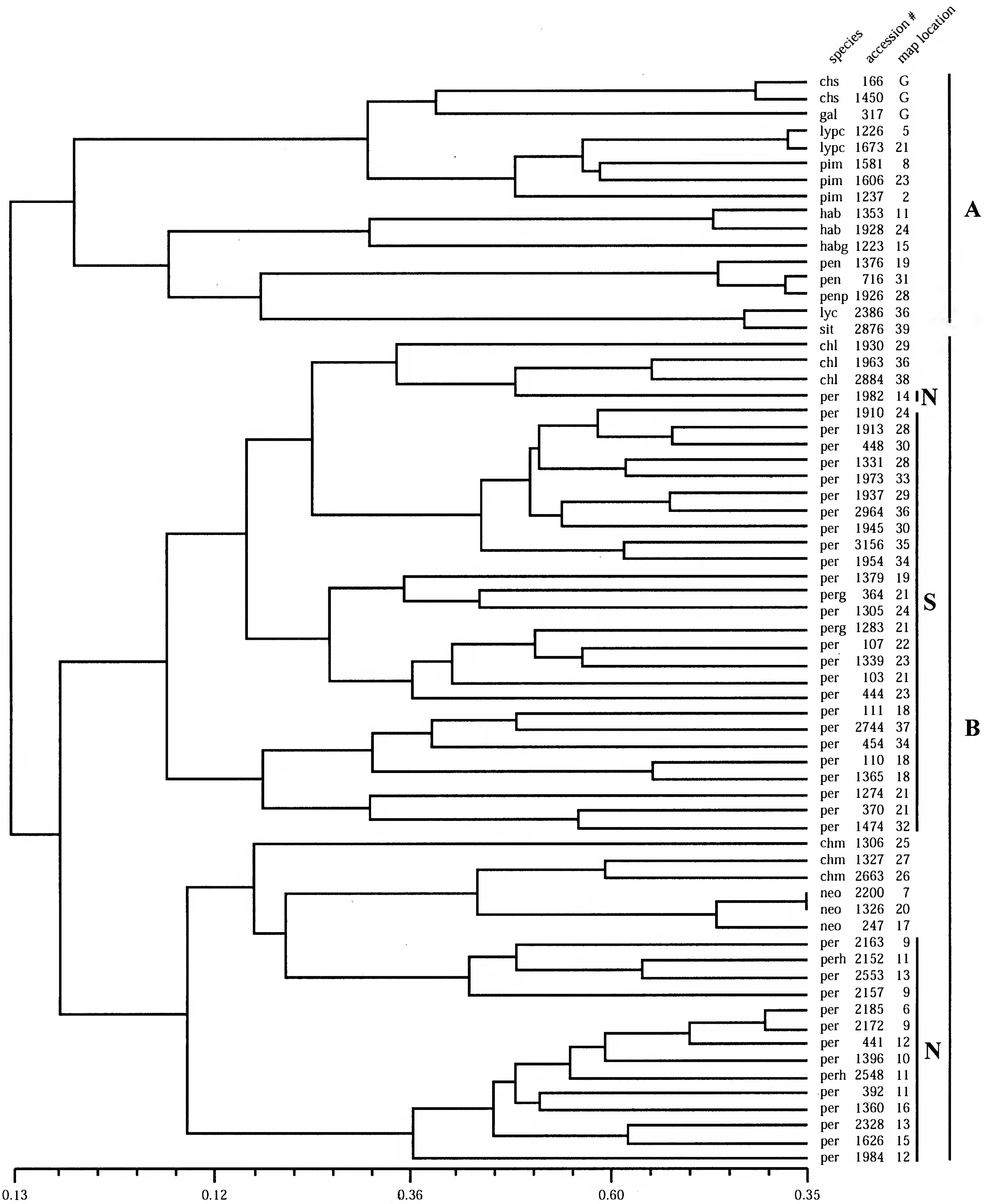
species
accession #
map location
chs 166 G
chs 1450 G
gal 317 G
lypc 1226 5
lypc 1673 21
pim 1581 8
pim 1606 23
pim 1237 2
hab 1353 11
hab 1928 24
habg 1223 15
pen 1376 19
pen 716 31
penp 1926 28
lyc 2386 36
sit 2876 39
chl 1930 29
chl 1963 36
chl 2884 38
per 1982 14
per 1910 24
per 1913 28
per 448 30
per 1331 28
per 1973 33
per 1937 29
per 2964 36
per 1945 30
per 3156 35
per 1954 34
per 1379 19
perg 364 21
per 1305 24
perg 1283 21
per 107 22
per 1339 23
per 103 21
per 444 23
per 111 18
per 2744 37
per 454 34
per 110 18
per 1365 18
per 1274 21
per 370 21
per 1474 32
chm 1306 25
chm 1327 27
chm 2663 26
neo 2200 7
neo 1326 20
neo 247 17
per 2163 9
perh 2152 11
per 2553 13
per 2157 9
per 2185 6
per 2172 9
per 441 12
per 1396 10
perh 2548 11
per 392 11
per 1360 16
per 2328 13
per 1626 15
per 1984 12
A
N
S
B
N
0.13
0.12
0.36
0.60
0.35

Figure 7. UPGMA dendrogram (CORR similarity option) based on 61 morphological characters. Species codes, accession numbers, and map locations as in Table 1.

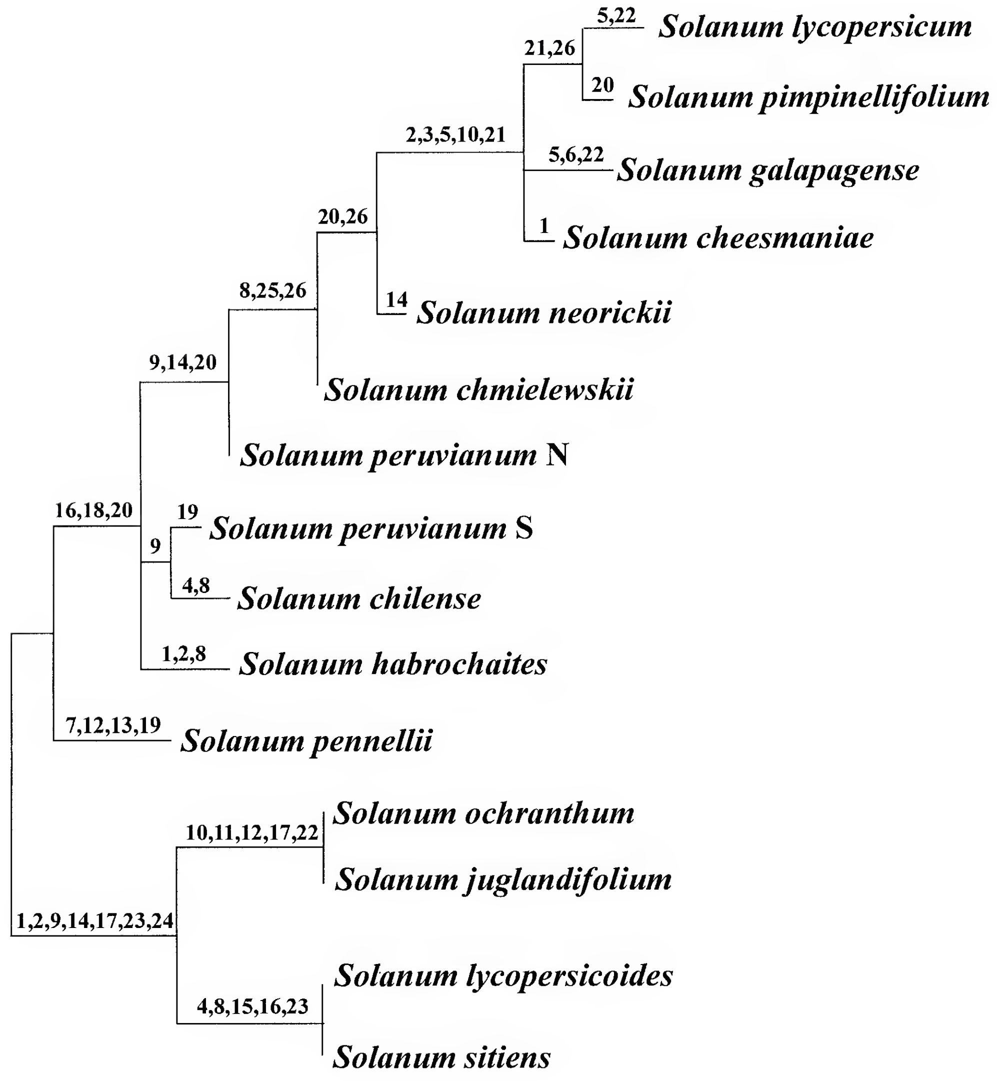
5,22
Solanum lycopersicum
21,26
20
Solanum pimpinellifolium
2,3,5,10,21
5,6,22
Solanum galapagense
20,26
1
Solanum cheesmaniae
8,25,26
14
Solanum neorickii
9,14,20
Solanum chmielewskii
Solanum peruvianum N
16,18,20
19
9
Solanum peruvianum S
4,8
Solanum chilense
1,2,8
Solanum habrochaites
7,12,13,19
Solanum pennellii
Solanum ochranthum
10,11,12,17,22
Solanum juglandifolium
1,2,9,14,17,23,24
Solanum lycopersicoides
4,8,15,16,23
Solanum sitiens

Figure 8. One representative phylogram of 28 equally parsimonious trees, length = 54, based on all 26 unordered morphological characters. CI = 0.870, CIU = 0.857, RI = 0.900.

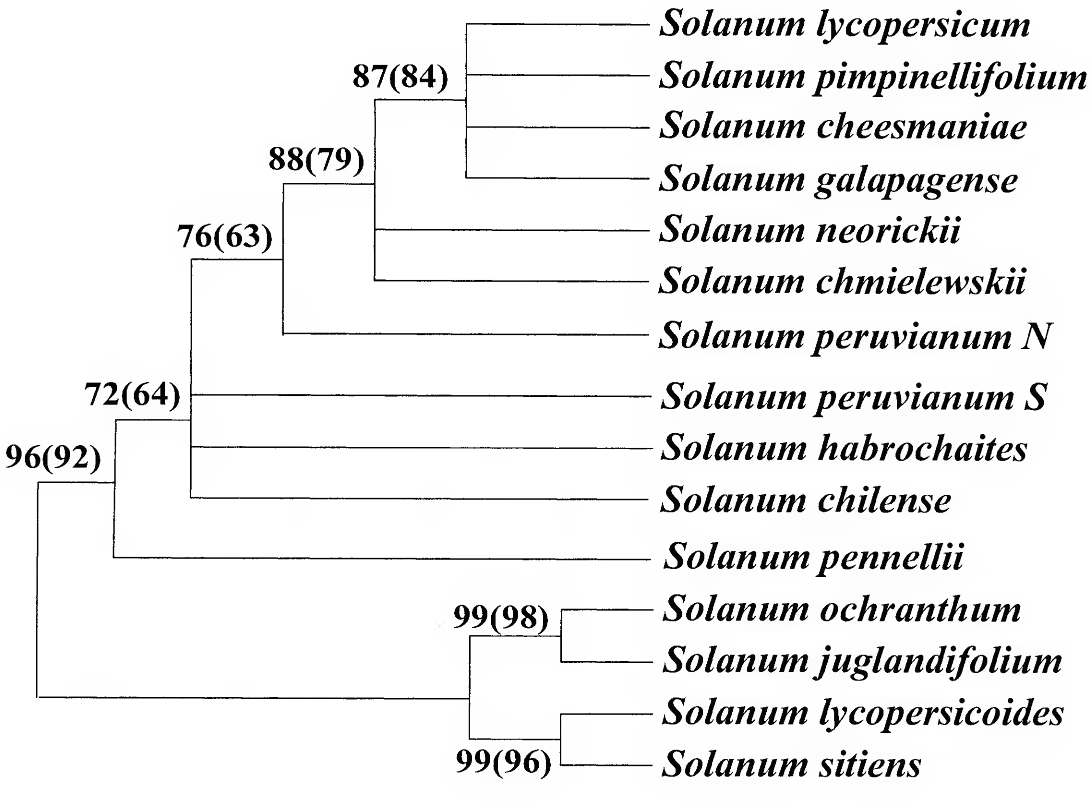
Solanum lycopersicum
87(84)
Solanum pimpinellifolium
Solanum cheesmaniae
88(79)
Solanum galapagense
76(63)
Solanum neorickii
Solanum chmielewskii
Solanum peruvianum N
72(64)
Solanum peruvianum S
96(92)
Solanum habrochaites
Solanum chilense
Solanum pennellii
99(98)
Solanum ochranthum
Solanum juglandifolium
Solanum lycopersicoides
99(96)
Solanum sitiens

Figure 9. Strict consensus tree of the 28 most parsimonious trees (length 54) based on all 26 unordered morphological characters. Percentage of 10,000 bootstrap replicates, followed by percentage of 10,000 jackknife replicates (in parentheses), is given above branches. The same strict consensus topology was obtained in the analysis excluding the two breeding characters, and nearly the same topology (except for *S. peruvianum* N that was part of the basal polytomy with *S. peruvianum* S, *S. habrochaites,* and *S. chilense*) in the analysis of 15 characters (25, 26, Tables 3, 4).

folium, and *S. lycopersicum*. (5) The self-incompatible *S. chilense*, *S. habrochaites*, and *S. peruvianum* south form a basal polytomy in the ingroup (the 15-character data set included *S. peruvianum* north in this basal polytomy).

CONCORDANCE OF MORPHOLOGICAL PHENETICS AND CLADISTICS

The phenetic results are not designed to show phylogenetic relationships. When similarities due to shared ancestral characteristics or homoplasy exceed similarities due to shared derived characteristics, the phenogram will not represent the true phylogeny, but if there were no homoplasy, the phenogram constructed by the phenetic analysis would correspond to the true phylogenetic tree (Futuyma, 1998). The similarities of phenetic and cladistic results show: (1) The outgroup taxa were differentiated in both analyses. (2) *Solanum cheesmaniae*, *S. galapagense, S. pimpinellifolium*, and *S. lycopersicum* were also consistent "groups." (3) *Solanum peruvianum* was differentiated in two groups from northern and southern Peru, with 76% bootstrap support in the cladistic results (Fig. 9). (4) *Solanum chmielewskii* and *S. neorickii* grouped with the northern *S. peruvianum* but not with *S. cheesmaniae*, *S. galapagense, S. pimpinellifolium*, and *S. lycopersicum* as in the cladistic results. (5) *Solanum chilense* grouped with the southern *S. peruvianum* in the phenetic results (Fig. 7), but in the cladistic results *S. chilense* appeared as a basal polytomy with southern *S. peruvianum* and *S. habrochaites* (Fig. 9).

CONCORDANCE OF MORPHOLOGICAL CLADISTICS AND GBSSI CLADISTICS

There are striking concordances between the morphological cladistic results shown here and the GBSSI cladistic results of Peralta and Spooner (2001). (1) Within the four outgroup taxa, *Solanum ochranthum* and *S. juglandifolium* were sister taxa and *S. lycopersicoides* and *S. sitiens* were sister taxa. (2) Within the tomato ingroup, *S. pennellii* was supported as a basal taxon. (3) *Solanum habrochaites* also appeared in a basal position. (4) *Solanum peruvianum* south showed a close relation with the last two taxa and also with *S. chilense*. (5) *Solanum cheesmaniae*, *S. galapagense*, *S. pimpinellifolium*, and *S. lycopersicum* were terminal taxa and monophyletic. (6) *Solanum chmielewskii* and *S. neorickii* were basal to *S. cheesmaniae*, *S. galapagense, S. pimpinellifolium*, and *S. lycopersicum*. GBSSI and morphological results showed a closer relationship of these three last taxa with *S. chmielewskii* and *S. neorickii*, which are also related to the northern populations of *S. peruvianum*.

DISCUSSION

PHENETICS

The above analysis of character state variation and phenetic relationships provided useful data to (1) help support existing species, (2) support the northern and southern populations of *Solanum peruvianum* as separate taxa, (3) show character state variation useful for species descriptions, and (4) show character states useful for cladistic analyses.

Although the range of values for many characters did not show discrete breaks to differentiate species, some have breaks in variability useful for species differentiation and cladistic analysis. The most important morphological characters, determined by the simple statistics and SDA, agreed with those previously used in taxonomic diagnoses and construction of keys (Müller, 1940; Luckwill, 1943; Rick et al., 1977, 1990; Taylor, 1986). Qualitative flower character states, such as white, free anthers with large filaments, and more than five leaves per sympodium were only shared by the species of subsection *Lycopersicoides*. Development of pseudostipules and inflorescence bracts, number of inflorescence branches, anther curvature, color and pubescence of the fruits, and trichome types have taxonomic value within wild tomatoes. *Solanum pennellii* traditionally has been recognized by its particular anther structure, lacking the sterile tip, poricidal dehiscence, and slightly asymmetric flowers.

Although most of the quantitative characters evaluated had continuous distribution of states across taxa, some of them were useful for species diagnosis. Short plants with short internode lengths and early formation of inflorescence (8th to 9th node) characterize *Solanum cheesmaniae*, while in the shrubby, low-branched, and taller plants of *S. lycopersicoides*, inflorescences were generated after the 35th node. *Solanum sitiens* can be identified by its smaller and narrow leaflets. *Solanum neorickii* was recognized by its small flowers with short anther tips, short inflorescence axis, and a high number of flowers in relation to the axis length. Diagnostic characters for *S. chilense* were large peduncles, leaves with few secondary and tertiary leaflets, and large flowers and fruits. Taller, very robust, and pubescent plants characterized *S. habrochaites*, which produces inflorescences after the 18th node, and has leaves without secondary leaflets. In *S. pennellii*, the width of the leaflet lamina, as well as anther length and structure, are valuable diagnostic characters. *Solanum lycopersicum* produced the largest fruits and numerous secondary leaflets, while *S. pimpinellifolium* presented the largest ratio between corolla lobe length and corolla lobe width, indicating a stellate shape.

The phenetic analysis distinguished the "northern" and "southern" groups in *S. peruvianum*. This result was postulated by morphology and crossing relationships (Rick, 1963, 1979, 1986b), and was also supported by the GBSSI phylogeny on the same accessions (Peralta & Spooner, 2001). The SDA selected similar sets of characters to those used previously to characterize the northern races, such as unbranched inflorescence, straight anther tubes, reduced style exsertion, and 5 to 7 leaflets (Rick, 1986b). Although most of the quantitative characters had a continuous distribution of states across these northern and southern populations, some of them (plant height, internode length, inflorescence axis length, leaf length, size of leaflets, and sepal length) showed that taller and more robust plants characterized the northern accessions. In contrast, the southern accessions can be differentiated by the presence of few secondary leaflets, branched inflorescences, bright yellow larger corollas, bright yellow larger and curved anthers, and exserted styles.

CLADISTICS

Concordance among phenetic and cladistic results might indicate that the amount of homoplasy does not outnumber similarities due to shared derived characteristics in wild tomatoes. The following discussion focuses on cladistic results of morphological, GBSSI, and other molecular data to comment on prior phylogenetic hypotheses in tomatoes (above). Cladistic results of morphological features confirm ingroup relationships shown by nuclear RFLP data (Miller & Tanksley, 1990), cpDNA restriction site data (Palmer & Zamir, 1982), and GBSSI DNA sequence data (Peralta & Spooner, 2001). Phenetic and cladistic analyses of morphological characters showed the distinct nature of the northern and southern Peruvian populations of *Solanum peruvianum*, a result consistent with GBSSI sequence data. The morphology shown here, as well as the nuclear RFLP (Miller & Tanksley, 1990), cpDNA restriction site (Palmer & Zamir, 1982), and GBSSI data (Peralta & Spooner, 2001), do not agree with the mitochondrial DNA phenetic results (McClean & Hanson, 1986).

Monophyly of the self-compatible species with pigmented fruits, *Solanum cheesmaniae, S. galapagense*, *S. pimpinellifolium*, and *S. lycopersicum*, has been shown by the cpDNA phylogeny, GBSSI data, and nuclear RFLP data, and here confirmed by morphology. Furthermore, *S. neorickii* and *S. chmielewskii* were placed with northern races of *S. peruvianum* as recently shown by cpDNA, nuclear RFLP, and GBSSI data. *Solanum chmielewskii* and *S. neorickii* appeared supported together in a basal position in the same clade as *S. cheesmaniae*, *S. galapagense, S. pimpinellifolium*, and *S. lycopersicum*. Our morphological and GBSSI results showed the northern accessions of *S. peruvianum* as closely related to *S. neorickii*, *S. chmielewskii*, and the three red- to orange- to yellow-fruited species of the Esculentum complex, discordant with Rick's (1979) classification (Fig. 1). Furthermore, the morphological results, as well as cpDNA, nuclear RFLP, and GBSSI data, are discordant with the placement of *S. pennellii* and *S. habrochaites* in the Esculentum group (Rick, 1979). On the other hand, *Solanum chilense* showed close relationships with the southern accessions of *S. peruvianum*, as indicated by crossability (Rick, 1979), cpDNA, and GBSSI phylogeny.

Morphological and molecular data support allogamy, self-incompatibility, and green fruits as plesiomorphic in tomatoes. The basal taxa also share characters such as branched and bracted inflorescences and leaves usually with pseudostipules. These results do not support the phylogenetic hypothesis proposed by Luckwill (1943), where all tomato species evolved from an ancestral stock with unbranched inflorescences, leaves with few leaflets, and without pseudostipules.

Large and attractive flowers have also been associated with the presence of a self-incompatibility system, and with the extent of outcrossing and genetic variation. Rick (1982b) postulated that three independent genetic systems are operating on the prevention of self-fertilization, changes in flower parts to ensure cross pollination, and development of secondary flower display characters to attract pollinators. Interestingly, a recent linkage analysis and quantitative trait loci (QTL) mapping of reproductive behavior and floral traits in wild tomatoes showed that major QTLs for several characters important to pollination biology harbor in the same region of the self-incompatibility locus, S, on chromosome 1. These QTL results suggest that a gene complex is controlling both genetic and morphological mechanisms of reproduction, and this gene complex may have been conserved since early periods of plant evolution or may reflect a convergent evolutionary process (Bernacchi & Tanksley, 1997).

Several characters of the corolla, anthers, and stigma (Table 2), associated with floral display, pollinator attraction, and reproduction, were included in this morphological study. The self-incompatible accessions of *S. habrochaites* and *S. pennellii* (Table 1) showed larger corollas and anthers as well as more exserted stigmas than the self-compatible accessions. Similarly, in the self-compatible *S. pimpinellifolium* one facultative allogamous accession has larger flower parts and stigma exsertion than the two autogamous accessions. Changes in flower size and stigma exsertion also occur in the two sibling self-compatible species, *S. chmielewskii* and *S. neorickii*. The accessions of the first species showed larger flower parts, while the accessions of the exclusively autogamous *S. neorickii* have smaller flower parts and stigmas included in the anther tube. The southern self-incompatible accessions of *S. peruvianum*, like the outcrossing genotypes of *S. habrochaites*, *S. pennellii*, and *S. pimpinellifolium*, also displayed floral traits for pollination attraction. Larger, bright yellow corollas, larger, curved and asymmetrical anthers, and exserted styles are features that probably correlate with the high outcrossing rates found in *S. peruvianum* (Rick et al., 1977). Actually, branched inflorescences with many showy open flowers (usually 8 to 10) act as the attractive unit for pollinators (Rick et al., 1978). In contrast, the northern *S. peruvianum* accessions have unbranched inflorescences, smaller corollas, short and straight anther tubes, and reduced stigma exsertion. The differences found in inflorescence and flower morphology, and crossing behavior between northern and southern *S. peruvianum* races, raise an interesting question about the role that environmental factors might play in such differentiation. Northern races are widespread from the coast to interior uplands in the Andes (north of 8°S) in more mesic-subtropical habitats (Rick, 1986b). In contrast, the southern races are distributed along the arid Pacific coast (south of 8°S) to northern Chile, and in the adjacent Andean Mountains (Rick, 1986b). The present hyper-arid climates between 5°S and 28°S result primarily from the rain shadow effects of the Andes and the subtropical convergence of winds, and the drying effects of the cold Humboldt Current. Paleobotanical, paleontological, and geological evidences suggest that such harsh climatic conditions developed recently during the Holocene (Arroyo et al., 1988). The Neotropical plant communities that occupied the area before the climatic change were displaced toward more southerly and boreal latitudes, and a new flora became adapted to the new xeric conditions (Villagran et al., 1983). A similar scenario can be hypothesized to explain the differentiation between *S. peruvianum* groups. The southern populations became adapted to the unstable, very arid conditions of the coastal Pacific range. Under such harsh climatic conditions, lower pollinator availability and an increase of anemophily in the plant communities have been reported (Arroyo et al., 1983). Selection pressures to ensure crossing in self-incompatible plants may have driven changes in flower traits that increase insect attraction. The shifts of secondary flower characters are correlated with increase in levels of heterozygosity in populations (Rick et al., 1977). An opposite change toward reduction of flower organs and attractiveness has been reported in the self-compatible *S. cheesmaniae*. This endemic species of the Galápagos Islands grows in isolated, unstable, and dry habitats, where very few pollinator species are found. The *S. cheesmaniae* populations evolved toward strict autogamy, and genetic variation was only found between populations (Rick, 1986b).

Genetic mechanisms ensuring crossing may have played a role to maintain gene flow among southern *S. peruvianum* populations, as has been supported by hybridization studies (Rick, 1963, 1979, 1986b). In contrast, the northern populations growing in more stable habitats developed isolation mechanisms that prevent gene flow in sympatric populations. In addition to the prezygotic barriers, postzygotic isolating mechanisms have been found in this group (Ehlenfeldt & Hanneman, 1992).

A possible scenario in the evolution of wild tomatoes can be hypothesized taking into account the adaptation to changing environments, as well as the interaction with biotic factors such as availability of pollinators. The shift toward compatibility and reduction of floral structures also played an important role in the speciation process. Putative SI ancestral populations probably occupied a wide area of distribution in central Peru. After the drastic climatic change during the Holocene and the formation of the Peruvian–Chilean desert, a process of adaptation to the new habitats may have occurred leading to differentiation and speciation. Some populations, adapted to more mesic and humid conditions, colonized the northern areas. Changes from SI to SC may have originated autogamous populations, further accentuating isolation and probably genetic drift, and contributed to differentiation and speciation. Putative ancestors from the Rio Marañón area may have originated self-compatible taxa, as suggested by Rick (1986b). On the other hand, populations growing in arid habitats may have differentiated and migrated following the Pacific coast and colonized the adjacent western slopes, but were limited in their altitudinal distribution by frost. Selection pressure to ensure crossing in the SI populations may have driven evolutionary changes, and genetic differentiation most probably occurred by gene substitution (Rick, 1986b). Reproductive isolating barriers arose to prevent gene flow between sympatric populations. Analogously, putative ancestors of *S. juglandifolium* and *S. ochranthum* became adapted to more wet and warm environments, while ancestors of *S. sitiens* and *S. lycopersicoides* evolved in the desert.

Some taxonomic problems remain, and more studies are needed to elucidate the relationships between *Solanum chmielewskii* and the northern *S. peruvianum* races, and between *S. chilense* and the southern *S. peruvianum* races. Palmer and Zamir (1982), based on a cpDNA phylogeny, suggested that *S. chmielewskii* and *S. chilense* could be considered at the subspecific level within *S. peruvianum*. Müller (1940) considered *S. chilense* as a variety of *S. peruvianum*, while Luckwill (1943) included it as the subspecies *puberulum*. Our morphological results, based on few *S. chmielewskii* and *S. chilense* accessions, provided good diagnostic characters. Nevertheless, analysis of more collections and herbarium specimens, especially those from original types, will help to clarify taxonomic problems. Studies of *S. peruvianum* infraspecific categories as well as the species recognized as *L. glandulosum* and *L. pissisi* are currently in progress. Rick and Lamm (1955), based on the photograph of the original collection of *L. pissisi*, concluded that this specimen was not related to *S. peruvianum*. Nevertheless, the identity of *L. pissisi* remains unsolved.

Our morphological results support existing species and support the northern and southern populations of *S. peruvianum* as separate taxa that may represent two distinct species.

Morphological data showed valuable diagnostic characters for species differentiation and phylogenetic relationships in wild tomatoes. These results are currently being used to prepare a monographic study of *Solanum* sections *Lycopersicon, Lycopersicoides,* and *Juglandifolium.* This monograph will include a new classification based on a synthesis of different data sets, reflecting the phylogenetic relationships of wild tomato species.

NOTE IN PROOF

This paper showed the need to reconsider the species limits of *Solanum peruvianum;* this was accomplished by Peralta et al. (2005) who recognized four species within *Solanum peruvianum* sensu lato, necessitating the publication of two new names.

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11

SYSTEMATICS OF *DEPREA* AND *LARNAX* (SOLANACEAE) BASED ON MORPHOLOGICAL EVIDENCE

Neil W. Sawyer

ABSTRACT. Cladistic analyses of morphological data were conducted to determine the monophyly of *Deprea* and *Larnax* (Solanaceae) and their phylogenetic relationships to other genera in tribe Physaleae. Character analysis resulted in 81 characters useful for phylogenetic analysis. Cladistic analysis of 20 genera with *Salpichroa* as outgroup yielded evidence that: (1) *Deprea* species are paraphyletic, but monophyletic with the transfer of *D. glabra* and *D. sylvarum* to *Larnax*; (2) *Larnax* species are monophyletic; (3) *Brachistus* is sister to *Deprea*; (4) *Aureliana* is sister to *Larnax*; (5) Brazilian *Athenaea* is sister to Old World *Withania*; (6) a broadly defined physaloid clade does not exist, the inflated, accrescent calyx typical of *Physalis* species having evolved at least three times; and (7) *Darcya spruceana* is aligned with *Aureliana* and ancestral to *Larnax*. Species of *Larnax* bearing plicate, *Physalis*-like calyces group within a largely Peruvian clade. Six synapomorphies distinguish *Larnax* from *Deprea*: filament length, filament adnation, filament base expansion, anther length, and pollen surface texture.

Key words: *Deprea*, *Larnax*, morphology, phylogeny, Physaleae, Solanaceae.

Deprea Raf. and *Larnax* Miers are Neotropical, Andean genera of the Solanaceae. They occur on sandy soils in premontane, montane, and cloud forests from Costa Rica to Bolivia. *Deprea* comprises six species and *Larnax* 22 (Sawyer, 2001), all suffruticose shrubs or small trees. Until recently they were placed in the large tribe Solaneae (34 genera; ~ 1500 species), which included taxa with two-loculate ovaries, including *Physalis* and its relatives (D'Arcy, 1991).

The monophyly of *Deprea* or *Larnax* has never been demonstrated using study of live material or modern cladistic methods. Further, there are surprisingly little data regarding intergeneric relationships between these and other so-called physaloid genera, genera possessing a *Physalis*-like calyx in fruit. Taxonomic confusion has pervaded at the genus level as evidenced by the historic shuffling of *Deprea* and *Larnax* among seven genera (Table 1). D'Arcy (1993a) merged *L. subtriflora*, the type species of *Larnax*, with *Deprea*, thus merging the genera. The following year, Barboza and Hunziker (1994) described six characters from study of museum material that served to delimit *Deprea* and *Larnax* (Table 2). However, my field studies (Sawyer, 1999a) revealed that four of these characters had overlapping character states (venation patterns in calyx lobes, corolla form, the degree of filament base expansion (= stamen petalum) (see Barboza & Hunziker, 1991; Ritterbusch, 1991; Barboza & Hunziker, 1994), the presence or absence of appendices on the stamen petalum), and the remaining two characters exhibited continuous quantitative variation across the genera (ratio of corolla limb length to tube length and the ratio of filament length to anther length).

It has been suggested that sister taxa to *Deprea* or *Larnax* should be found among genera associated with *Physalis* L. with which *Deprea* and *Larnax* previously have been aligned (Averett, 1979; D'Arcy, 1979; Axelius, 1996; Estrada & Martínez, 1999). Several genera share traits with *Deprea* and *Larnax*, including the presence of a persistent, accrescent calyx that either closely invests or inflates around a fleshy berry (Averett, 1979; D'Arcy, 1979; Table 3). This trait is found in species of *Brachistus* (Kunth) Miers (D'Arcy, 1973; Gentry & Standley, 1974; Hunziker, 1969b), *Cuatresia* Hunz. (Hunziker, 1987; Sawyer, 1999b), *Iochroma* Benth. (Hunziker, 1977), *Physalis* and its immediate relatives (Martínez, 1993; Estrada, 1995), *Vassobia* Rusby (Hunziker, 1984), and *Withania* Pauq. (Pauquy, 1825; D'Arcy, 1979; Hepper, 1991). Of these, *Brachistus* and *Withania* share valvate corolla aestivation with *Deprea* and *Larnax*. However, unlike *Deprea* and *Larnax*, species of *Brachistus* and *Withania* have thick, non-compressed seeds. *Physalis* (Martínez, 1993) and its close relatives (*Chamaesaracha* Benth., *Leucophysalis* Rydb., and *Physaliastrum* Makino [D'Arcy & Zhi-yun, 1992]) and *Iochroma* possess plicate corolla aestivation. *Cuatresia* and *Vassobia* possess induplicate-valvate corolla aestivation (Baehni, 1946). *Aureliana* Sendt., a genus that Gabriel Bernadello (Universidad Nacional de Córdoba, Argentina, pers. comm.) considers closely related to *Larnax*, also possesses valvate corolla aestivation, and has many floral attributes in common with *Larnax*. However, the accrescent calyx so distinctive of *Larnax* species is lacking in *Aureliana*.

Cladistic evidence for the resolution of relationships between *Deprea* and *Larnax* and related genera is derived from chloroplast DNA restriction site mapping (Olmstead & Palmer, 1992; Martínez, 1993), *ndh*F chloroplast DNA sequences (Olmstead et al., 1999), morphology (Axelius, 1996; Estrada & Martínez, 1999), and chemotaxonomy (Tétényi, 1987). Martínez (1993) included a single species, *D. paneroi*, as an outgroup in her restriction site mapping study of *Physalis* and placed *D. paneroi* outside a *Physalis* clade (*Withania* is not represented). The studies of Axelius (1996) and Estrada and Martínez (1999) attempted to clarify relationships among physaloid genera. Although both these morphology-based studies include species of *Deprea* and *Larnax*, neither provides a complete picture of intergeneric relationships. In addition to species of *Physalis* and closely related genera, Axelius (1996) included a single species each of *Deprea* and *Larnax* and several species of *Withania*. Many characters for *Deprea* and *Larnax* were scored as missing data or, as my field-collected data revealed (Sawyer, 1999a), were scored incorrectly. The consequently ambiguous results place unresolved *Deprea* and *Larnax* in a clade sister to *Withania*. Estrada and Martínez (1999), in their limited study of physaloid genera, included two species of *Deprea* and *L. sachapapa*. Results of this study likewise were unable to resolve the phylogenetic placement of *Deprea* or *Larnax*, but suggest the sister to these genera is *Tzeltalia* E. Estrada & Martínez, a genus consisting of two recently segregated species of *Physalis* (Estrada & Martínez, 1998). Tétényi (1987) included *Withania* among the physaloid genera in his chemotaxonomic treatment of the Solanaceae. The discovery by Echeverri et al. (1988) of a withanolide steroid in *D. orinocensis*, a compound known to occur in *Withania* and *Witheringia* L'Hér., seems to suggest a relationship between these genera. *Deprea* and *Larnax* are unrepresented in the otherwise comprehensive *ndh*F sequence data of Olmstead et al. (1999). Consequently, it is difficult to determine their relationship to other members of a large clade (tribe Physaleae), some of whose members possess accrescent calyces, such as *Withania* (see Axelius, 1996) and *Physalis* (see Estrada & Martínez, 1998). Making these determinations is further frustrated by the absence of sequence data for other possibly related genera, e.g., *Athenaea* Sendt., *Brachistus*, and *Cuatresia* (Olmstead et al., 1999).

None of the studies mentioned above includes *Athenaea* or *Cuatresia*. Very little is known of the affiliations of *Cuatresia*, a genus whose members possess accrescent calyces, but none are plicate-ribbed or invaginated as those of *Physalis*. The Brazilian endemic *Athenaea* has been associated with *Deprea* (Standley, 1935; Werdermann, 1937; Standley & Morton, 1938) and *Larnax* (Zahlbruckner, 1892) (Table 1). However, unlike *Deprea* or *Larnax*, species of *Athenaea* possess leaf-like fruiting calyces that, although accrescent, do not inflate around or closely invest the fruit (Barboza & Hunziker, 1989; Hunziker, 1969a, 1969b).

Only Estrada and Martínez (1999) included *Brachistus*. Morphology-based work of Sousa-Peña and Anderson (pers. comm.) demonstrates a close relationship between *Witheringia* and *Brachistus*. Corollas of *Witheringia* possess varying degrees of valvate or induplicate-valvate aestivation and, although the calyx can be accrescent, it never envelops the berry (Hunziker, 1969a, 1969b, 1971; Sousa-Peña, pers. comm.).

Cladistic analyses using morphological data (Axelius, 1996; Estrada & Martínez, 1998) suggest that *Physalis*, *Withania*, *Deprea*, and *Larnax* are members of a physaloid clade. However, the fact that only 2 of 10 *Withania* and 3 of 21 *Larnax* possess the calyx typical of most *Physalis* species and its close relatives (Hepper, 1991; Sawyer, 2001) suggests that a physaloid grouping is an artificial construct.

This study utilizes 28 species of *Deprea* and *Larnax* to address their relationships—*Deprea* to *Larnax* and phylogenetic placement with related genera in tribe Physaleae. Comparative morphological data are scored for use in cladistic analyses, and the resulting phylogenetic hypotheses are used to address several questions: (1) Are *Deprea* and *Larnax* each monophyletic and, if so, which characters delimit them? How do these conclusions affect their generic classification? (2) What are the intrageneric relationships in *Deprea* and *Larnax*? (3) Which genera in tribe Physaleae are closely aligned with *Deprea* and *Larnax*? (4) What are the intergeneric relationships within tribe Physaleae? (5) Does a definable physaloid clade exist?

Table 1.

List of *Deprea* or *Larnax* species as accepted herein with chronological nomenclatural history used by previous authors.

Deprea orinocensis	1818 Humboldt, Bonpland, Kunth	*Physalis orinocensis*
	1838 Rafinesque	*Deprea orinocensis*
	1849 Miers	*Larnax orinocensis*
	1852 Dunal	*Withania orinocensis*
	1973 D'Arcy	*Deprea orinocensis*
D. bitteriana	1937 Werdermann	*Athenaea bitteriana*
	1974 Benítez	*Withania bitteriana*
	1989 Barboza & Hunziker	*Deprea granulosa*
	1998 Sawyer & Benítez	*Deprea bitteriana*
D. cardenasiana	1977 Hunziker	*Deprea cardenasiana*
D. ecuatoriana	1996 Barboza & Hunziker	*Deprea ecuatoriana*
D. glabra	1935 Standley	*Athenaea glabra*
	1977 Hunziker	*Deprea glabra*
	2001 Sawyer	*Larnax glabra*
D. granulosa	1848 Miers	*Hebecladus granulosus*
	1998 Sawyer & Benítez	*Deprea orinocensis*
D. paneroi	1992 Benítez & Martínez	*Deprea paneroi*
	1993 Axelius & D'Arcy	*Deprea hirtifolia*
	1994 Barboza & Hunziker	*Deprea paneroi*
D. sylvarum	1938 Standley & C. V. Morton	*Athenaea sylvarum*
	1977 Hunziker	*Deprea sylvarum*
	2001 Sawyer	*Larnax sylvarum*
D. xalapensis	1818 Humboldt, Bonpland, Kunth	*Physalis xalapensis*
	1849 Miers	*Larnax xalapensis*
	1973 D'Arcy	*Deprea orinocensis*
Larnax subtriflora	1799 Ruiz & Pavón	*Physalis subtriflora*
	1849 Miers	*Larnax subtriflora*
	1852 Dunal	*Withania subtriflora*
	1892 Zahlbruckner	*Athenaea subtriflora*
	1962 MacBride	*Withania subtriflora*
	1977 Hunziker	*Larnax subtriflora*
	1993a D'Arcy	*Deprea subtriflora*
	2001 Sawyer	*Larnax subtriflora*
L. andersonii	1998 Sawyer	*Larnax andersonii*
L. cuyacensis	2001 Sawyer	*Larnax cuyacensis*
L. darcyana	2001 Sawyer	*Larnax darcyana*
L. dilloniana	1998a Leiva et al.	*Larnax dilloniana*
L. grandiflora	2001 Sawyer	*Larnax grandiflora*
L. harlingiana	1995 Barboza & Hunziker	*Larnax harlingiana*
L. hawkesii	1977 Hunziker	*Larnax hawkesii*
L. hunzikeriana	1995 Benítez & Martínez	*Larnax hunzikeriana*
	1999b Sawyer	*Cuatresia hunzikeriana*
L. longipedunculata	1998b Leiva et al.	*Larnax longipedunculata*
L. macrocalyx	1998b Leiva et al.	*Larnax macrocalyx*
	2001 Sawyer	*Larnax longipedunculata*
L. lutea	1996 Leiva	*Larnax lutea*
L. parviflora	2001 Sawyer	*Larnax parviflora*
L. peruviana	1892 Zahlbruckner	*Athenaea peruviana*
	1962 MacBride	*Withania peruviana*
	1977 Hunziker	*Larnax peruviana*
L. psilophyta	1998 Sawyer	*Larnax psilophyta*
L. pilosa	1998b Leiva et al.	*Larnax pilosa*
	2001 Sawyer	*Larnax sachapapa*
L. purpurea	1996 Leiva	*Larnax purpurea*
L. sachapapa	1977 Hunziker	*Larnax sachapapa*
L. sagasteguii	1998a Leiva et al.	*Larnax sagasteguii*
L. sawyeriana	1998b Leiva et al.	*Larnax sawyeriana*
L. steyermarkii	1977 Hunziker	*Larnax steyermarkii*
L. suffruticosa	1905 Dammer	*Iochroma suffruticosa*
	1977 Hunziker	*Larnax suffruticosa*
L. vasquezii	1998b Leiva et al.	*Larnax vasquezii*

TABLE 2.

Characters used to delimit *Deprea* and *Larnax*, modified from Barboza and Hunziker (1994).

Character	*Larnax*	*Deprea*
Venation of the calyx lobes	Venation pattern formed solely by the principal nerve or by the principal nerve and 1 or 2 small secondary or tertiary nerves	Venation pattern formed by 3 nerves: the principal nerve and 2 secondary nerves among a network of tertiary nerves
Corolla form	Rotate	Infundibular
Corolla limb: tube length	Lobes 2–4 times longer than the tube; exceptionally equal in *L. cuyacensis*, *L. glabra*, *L. longipedunculata*, *L. peruviana*, and *L. sylvarum*	Lobes always shorter than the tube
Relation of filament length to anther length	Filaments $\leq$ 55% the length of the anthers	Filaments > 140% the length of the anthers
Staminal part of the stamen petalum	Formed by the completely expanded filament	Filament base almost always expanding with limited development elsewhere; less frequently, the filament not expanding completely
Tooth-like appendices on the stamen petalum	Present or absent	Always absent

TABLE 3.

Accrescent calyx types among genera of tribe Physaleae. Calyx not enveloping fruit = 1; calyx leaf-like = 2; calyx enveloping and appressed to fruit = 3; calyx enveloping and inflated around fruit = 4. Taxa traditionally treated as "physaloid" indicated (* & in bold).

Genus	Calyx Type
Archiphysalis D'Arcy & Zhi-yun (1992)	4
Athenaea Hunziker (1989)	2
Brachistus Sousa-Peña & Anderson (unpubl.)	1, 3
Chamaesaracha* Averett (1973); D'Arcy (1991)	3
Cuatresia Hunziker (1987)	1, 3, 4
Deprea* Sawyer (unpubl.)	3, 4
Dunalia D'Arcy (1991)	1
Iochroma Hunziker (1977)	3
Larnax* Sawyer (2001)	3, 4
Margaranthus* Martínez (1993)	4
Leucophysalis* Averett (1979)	4
Oryctes* D'Arcy (1979)	4
Physaliastrum D'Arcy & Zhi-yun (1992)	4
Physalis* Martínez (1993)	3, 4
Saracha Alvarez (1995)	1
Tzeltalia* Estrada & Martínez (1998)	4
Vassobia Hunziker (1984)	1, 3
Withania* Hepper (1991)	3, 4
Witheringia Sousa-Peña & Anderson (unpubl.)	1

MATERIALS AND METHODS

ACQUISITION OF PRELIMINARY DATA

Fieldwork was conducted in Costa Rica (1994), Venezuela (1996, 1997), Colombia (1995), Ecuador (1995, 1996), Peru (1996, 1997), and Bolivia (1996). Twenty-two of 29 species were observed in situ. Flowering and fruiting material was preserved in 70% alcohol for microscopic study. Herbarium vouchers were deposited at COL, CR, HAO, LOJA, MERF, MY, UCR, and CONN. Attempts to locate *Deprea ecuatoriana* (Ecuador, Peru), *Larnax lutea* (Peru), *L. steyermarkii* (Ecuador), and *D. cardenasiana* (Bolivia) in the field were unsuccessful. An undescribed species of *Deprea* and *L. darcyana* (Sawyer, 2001) are local endemics occurring in currently inaccessible regions of Colombia, and, therefore, only museum material of these species was studied.

Specimens from U.S., South American, and European herbaria were examined (A, AAU, COL, F, G, GH, HAO, HUA, K, LOJA, MERF, MO, MY, NY, QCA, QCNE, TEX, US, USJ, VEN, WIS; a list of specimens is available from the author upon request). Type, isotype, or paratype specimens of all described species were studied, as well as photos of the destroyed type material of *L. peruviana* (B) and *L. suffruticosa* (B). Initial concepts of *Deprea* and *Larnax* and a preliminary list of delimiting attributes were obtained from the literature.

Twenty-one genera, including all twelve included in the Olmstead et al. (1999) provisional classification of tribe Physaleae, are employed in the cladistic analysis. *Archiphysalis* Kuang, *Mellissia* Hook. f., *Nectouxia* Kunth, *Oryctes* S. Watson, *Physaliastrum*, and *Quincula* Raf. are excluded. These genera are not included in the Olmstead et al. (1999) analysis and/or were unavailable for study. With the exception of the large genus *Physalis*, specimens of individual species characterize the morphological variation present in each genus. All eight species of *Deprea*, including an undescribed species (*D.* sp. nov.) that I have recognized as distinct based on morphological analysis, and all 22 species of *Larnax* (see Sawyer, 1999b, 2001) are included in the cladistic analysis.

Cladistic analysis necessitates choosing one or several taxa as outgroups to polarize character states (Maddison et al., 1984; Watrous & Wheeler, 1981). Chloroplast DNA restriction site data (Olmstead & Palmer, 1992) suggest that a large clade of at least 14 genera, including *Deprea* and *Larnax*, has *Datura* L. at its base. More comprehensive sequence data from the *ndh*F chloroplast gene (Olmstead et al., 1999) suggest that this clade (tribe Physaleae) has *Salpichroa* Miers at its base with *Datura* lying much further out. Therefore, because Olmstead et al. (1999) is the most comprehensive (17 species in 13 genera) analysis to date, *Salpichroa tristis* Miers is used as the outgroup to polarize character states among the genera of tribe Physaleae.

SELECTION AND SCORING OF CHARACTERS

Guidance for initial character selection was provided by generic and specific descriptions from the primary literature. However, character selections were ultimately determined by comparative analyses of living, dried, and alcohol-preserved material. In cases where individual distinctions were desirable (e.g., between sibling species), autapomorphies were retained in the analysis.

Field studies were supplemented with study of museum collections from throughout the geographic range of each species. For *Deprea paneroi*, studies were supplemented by investigation of reproductive material from living greenhouse specimens. To avoid interpretive inconsistencies that may occur in scoring quantitative data (see Gift & Stevens, 1997), continuous quantitative or meristic traits were used for phylogenetic analysis only if they could be treated as qualitative characters, i.e., if their character state frequency distributions did not overlap among species (Stevens, 1991). In addition, quantitative characters were chosen to avoid non-independence (Felsenstein, 1985) and co-variance (Cain & Harrison, 1958).

All qualitative characters exhibiting variation among taxa were included in the cladistic analysis. To be consistent, the absence of a trait was scored as "0." Multi-state meristic characters were consistently scored with the highest datum equated with the lowest numbered character state. When character states were replicated for different characters, e.g., hair type choices among different leaf surfaces, they were repeated in the same order. Because all characters were scored as unordered and unweighted to avoid bias, it was not necessary to score multi-state qualitative characters in any particular order.

Unavailable data were scored as missing with a "?". Inapplicable data, i.e., cases where a character could be assessed for some species but not for others for reasons other than unavailability (e.g., character no. 39, attachment of pedicel to peduncle in Table 5, when a species with only a single flower lacks a peduncle vs. presence of a peduncle in species bearing several flowers), were scored as unknown with a "9." The use of "9" or another unassigned character state in these cases may be of concern, because, in the absence of a character, there is no way to assess homology. The inclusion of the states scored as "9" was weighed against the exclusion of the characters. Use of "9" for scoring inapplicable character states was justified by the recognized need to score inapplicable characters differently than missing or unknown character states (Maddison, 1993) and by the expected minimization of the homology problem among taxa that are closely related. Further, the scoring of character states with a "9" is used only in two characters among three genera, representing only 0.2% of the data. For polymorphic characters, i.e., characters represented by two or more character states in a species, all character states present in that species were scored. These are interpreted as polymorphic by PAUP. Ultimately, 81 characters were scored for cladistic analysis (Table 5).

DATA ANALYSIS

Data sets were analyzed using the maximum parsimony optimality criterion in PAUP* version 4.0.0b5 (Swofford, 2001). To avoid bias, character state changes were weighted equally and left unordered. An initial run was undertaken using 59 species among 20 genera, including *Salpichroa* as outgroup. All species of *Deprea* and *Larnax* (Table 1) were included. Because the data set was too large to allow use of exact search methods, a heuristic search was undertaken. To explore as many local optima as possible, 500 replicates of random stepwise addition were employed using the TBR branch swapping option. A heuristic search was then performed using the same parameters, including *Deprea*, *Larnax*, *Brachistus*, *Witheringia*, and *Aureliana*. For this analysis, *Aureliana* was defined as outgroup. All characters that were parsimony-uninformative due to constancy were excluded. Uninformative autapomorphies were retained. The taxon by character matrix for 59 species in 20 genera of tribe Physaleae used in these analyses is reported in Appendix I.

To estimate the robustness of the topology, decay analysis (Bremer, 1988; Donoghue & Sanderson, 1992) was performed using TBR branch swapping in the heuristic search option in PAUP with 100 replicates of stepwise random addition. The strict consensus of all trees one, two, three, or more steps longer than the most parsimonious tree(s) was computed, and the number of additional steps required to collapse any particular node. In addition, a bootstrap analysis (Felsenstein, 1985) was undertaken, employing 500 replicates in 100 replicates of stepwise random addition using TBR branch swapping.

Differences in character evolution among topologies and character state changes were investigated using MacClade version 3.04 (Maddison & Maddison, 1992). Alternate topologies were investigated by constraining trees in PAUP and determining the length of the topologies relative to those for the most parsimonious trees.

TABLE 4. Distribution and size of genera studied.

	North or Central America	Northwestern South America	Central America	Old World
Brachistus Sousa-Peña & Anderson (unpubl.)	3 spp.	—	—	—
Chamaesaracha D'Arcy (1991)	10 spp.	—	—	—
Leucophysalis D'Arcy (1991)	9 spp.	—	—	—
Margaranthus Martínez (1993)	1 spp.	—	—	—
Physalis Martínez (1993)	66 spp.	12 spp.	—	6 spp.
Tzeltalia Estrada & Martínez (1998)	2 spp.	—	—	—
Witheringia Sousa-Peña (pers. comm.)	16 spp.	5 spp.	—	—
Acnistus Hunziker (1979)	—	1 sp.	—	—
Cuatresia Hunziker (1987)	2 spp.	10 spp.	—	—
Dunalia Hunziker (1979)	—	6 spp.	—	—
Iochroma Hunziker (1979)	—	15 spp.	1 sp.	—
Salpichroa D'Arcy (1991)	—	15 spp.	—	—
Saracha Alvarez (1995)	—	2 spp.	—	—
Athenaea Barboza & Hunziker (1989)	—	9 spp.	—	—
Aureliana Hunziker & Barboza (1990)	—	5 spp.	—	—
Vassobia Hunziker (1984)	—	4 spp.	—	—
Tubocapsicum D'Arcy (1991)	—	—	—	1 sp.
Withania Hepper (1991)	—	—	—	10 spp.

TABLE 5. Scoring of morphological characters used in cladistic analyses.

1. Branchlet form: 0 = never flexuose; 1 = flexuose.
2. Stem prickles: 0 = absent; 1 = present.
3. Leaf arrangement at a node: 0 = unpaired; 1 = paired.
4. Heterophylly: 0 = absent; 1 = present.
5. Mean petiole length: 0 = > 26 mm; 1 = 4–18 mm; 2 = < 2 mm.
6. Leaf texture: 0 = membranous; 1 = fleshy.
7. Leaf margin shape: 0 = entire; 1 = dentate.
8. Leaf apex shape: 0 = acute; 1 = acuminate.
9. Leaf base shape: 0 = attenuate; 1 = cuneate; 2 = truncate-cordate.
10. Sessile glands of the adaxial leaf surface: 0 = absent; 1 = present.
11. Non-glandular hairs on the adaxial leaf surface: 0 = absent; 1 = present.
12. Glandular hairs on the adaxial leaf surface: 0 = absent; 1 = present.
13. Branched hairs on the adaxial leaf surface: 0 = absent; 1 = present.
14. Non-glandular hairs on the adaxial leaf veins: 0 = absent; 1 = present.
15. Glandular hairs on the adaxial leaf veins: 0 = absent; 1 = present.

16. Non-glandular hairs on the abaxial leaf surface: 0 = absent; 1 = present.
17. Glandular hairs on the abaxial leaf surface: 0 = absent; 1 = present.
18. Branched hairs on the abaxial leaf surface: 0 = absent; 1 = present.
19. Non-glandular hairs on the abaxial leaf veins: 0 = absent; 1 = present.
20. Glandular hairs on the abaxial leaf veins: 0 = absent; 1 = present.
21. Branched hairs on the abaxial leaf veins: 0 = absent; 1 = present.
22. Mean length of hairs: 0 = > 1.2 mm; 1 = < 0.9 mm.
23. Stalked pluricellular glands on vegetative plant body: 0 = absent; 1 = present.
24. Sessile glands on the corolla exterior: 0 = absent; 1 = present.
25. Non-glandular hairs on the corolla exterior: 0 = absent; 1 = present.
26. Glandular hairs on the corolla exterior: 0 = absent; 1 = present.
27. Branched hairs on the corolla exterior: 0 = absent; 1 = present.
28. Corolla exterior hair density (scarcely pubescent = 2–7 hairs/mm^2; pubescent = > 13 hairs/mm^2): 0 = glabrous; 1 = scarcely pubescent; 2 = pubescent.
29. Corolla annulus hair density (scarcely pubescent = 2–7 hairs/mm^2; pubescent = > 13 hairs/mm^2): 0 = glabrous; 1 = scarcely pubescent; 2 = pubescent.
30. Non-glandular hairs within the corolla annulus: 0 = absent; 1 = present.
31. Glandular hairs within the corolla annulus: 0 = absent; 1 = present.
32. Branched hairs within the corolla annulus: 0 = absent; 1 = present.
33. Filament pubescence: 0 = glabrous; 1 = base pubescent; 2 = pubescent entire length.
34. Sessile glands on the fruiting calyx interior: 0 = absent; 1 = present.
35. Stalked unicellular glands on the fruiting calyx interior: 0 = absent; 1 = present.
36. Stalked pluricellular glands on the fruiting calyx interior: 0 = absent; 1 = present.
37. Glandular hairs on the fruiting calyx interior: 0 = absent; 1 = present.
38. Peduncle attachment to stem and length: 0 = peduncle absent; 1 = free from stem and > 10 mm; 2 = free from stem and < 5 mm; 3 = fused to stem.
39. Pedicel attachment to peduncle: 0 = opposite; 1 = oblique.
40. Maximum flowers produced per node: 0 = > 9; 1 = 5–7; 2 = 3–4; 3 = 1–2.
41. Pedicel length: 0 = > 23 mm; 1 = < 20 mm.
42. Number of calyx lobes: 0 = five; 1 = four.
43. Corolla color: 0 = white or white/purple; 1 = yellow or yellow/purple; 2 = green or green/purple; 3 = purple.
44. Anthocyanins in the corolla: 0 = absent; 1 = present, expression invariable; 2 = present, expression variable.
45. Corolla aestivation: 0 = valvate; 1 = induplicate-valvate; 2 = plicate.
46. Thickness of corolla limb: 0 = > 0.3 mm; 1 = < 0.2 mm.
47. Mean corolla length: 0 = > 18 mm; 1 = < 14.5 mm.
48. Corolla limb length as a percentage of tube length: 0 = > 125%; 1 = 90–110%; 2 = 50–80%; 3 = < 50%.
49. Petal flexion: 0 = flexion absent; 1 = flared; 2 = rotate; 3 = reflexed.
50. Filament length: 0 = > 12 mm.; 1 = 5.8–9.3 mm; 2 = < 4.8 mm.
51. Filament size differences: 0 = equal; 1 = unequal.
52. Filament adnation: 0 = > 2.7 mm; 1 = < 1.8 mm.
53. Filament base: 0 = expanded; 1 = expanded with projections at the shoulders; 2 = narrowing from base; 3 = indistinctly adnate.
54. Apical appendages of the filament base: 0 = absent; 1 = present.
55. Filament attachment: 0 = dorsifixed; 1 = basifixed or ventrifixed.
56. Anther apiculum: 0 = absent; 1 = present.
57. Anther length: 0 = > 2.7 mm; 1 = 1.4–2.5 mm; 2 = < 1.2 mm.
58. Anther size differences: 0 = all equal in length; 1 = anthers in two or three size classes.
59. Anther length as a percentage of filament length: 0 = > 55%; 1 = < 45%.
60. Presence and type of calcium oxalate crystals in the pollen sac: 0 = absent; 1 = present as druses; 2 = present as blocks; 3 = present as aggregate druses.
61. Timing of style exsertion: 0 = after anthesis; 1 = prior to anthesis.
62. Stigma shape: 0 = clavate; 1 = sub-bilobate.
63. Fruiting calyx shape: 0 = urceolate; 1 = elliptic-fusiform; 2 = pyriform; 3 = invaginate-pyriform-plicate; 4 = planate.
64. Fruiting calyx shape: 0 = leaf-like; 1 = non-leaf-like.
65. Fruiting calyx investment: 0 = non-accrescent; 1 = accrescent, not enveloping fruit; 2 = accrescent, partially enveloping fruit; 3 = accrescent, fully enveloping fruit.
66. Fruiting calyx investment: 0 = no investment; 1 = appressed to fruit; 2 = inflated around fruit.
67. Fruiting calyx integrity: 0 = intact when mature; 1 = split by the expanding berry.
68. Fruiting calyx primary costa elevation: 0 = appressed to calyx; 1 = elevated above calyx surface.
69. Number of fruiting calyx costa: 0 = five prominent costa; 1 = five prominent primary, five prominent secondary costa.
70. Fruiting calyx maximum length * width: 0 = > 200 mm^2; 1 = 165–185 mm^2; 2 = 75–150 mm^2; 3 = 40–60 mm^2; 4 = < 30 mm^2.
71. Fruiting calyx margin shape: 0 = triangular lobed; 1 = triangular lobed with subulate veins; 2 = unlobed with subulate vein extensions; 3 = truncate; 4 = rounded-mucronate.
72. Fruiting calyx lobe maximum length: 0 = > 4 mm; 1 = 2.5 mm; 2 = 1.8–2 mm; 3 = 1.4–1.5 mm; 4 = 0.8 mm; 5 = 0.4–0.5 mm.
73. Calyx lobe length: 0 = equal in length; 1 = unequal in length; 9 = inapplicable.
74. Pedicel position from flowering to fruiting: 0 = pendent; 1 = assurgent.
75. Fruit type: 0 = fleshy berry; 1 = drupaceous berry.
76. Fruit shape: 0 = ovate; 1 = elongate-elliptic; 2 = pyriform.
77. Fruit color: 0 = orange; 1 = white; 2 = purple; 3 = green or yellow.
78. Presence of sclerotic fruit bodies: 0 = absent; 1 = present.
79. Seeds per fruit: 0 = > 130; 1 = 100–120; 2 = 60–80; 3 = 30–50; 4 = < 20.
80. Seed thickness: 0 = > 1 mm; 1 = < 0.5 mm.
81. Pollen surface texture: 0 = scabrate; 1 = psilate; 2 = rugulate; 3 = rugulate-reticulate.

RESULTS

Cladistic analysis using 20 genera with *Salpichroa* as the outgroup produced 166 most parsimonious trees with weak support (819 steps; CI = 0.164 [with autapomorphies]; RI = 0.502; Figs. 1, 2). The topology shows (1) an *Athenaea/Withania* clade (Withaninae) occurring at the base of the tree; (2) support for the transfer of *D. glabra* and *D. sylvarum* to *Larnax* (Sawyer, 2001) with *Aureliana* as sister to *Larnax*; (3) *Darcya spruceana* (Hunz.) Hunz. more closely aligned with *Aureliana* and *Larnax* than with *Brachistus*, *Chamaesaracha*, or *Physalis*; (4) *Physalis* and its close relatives, including *Tzeltalia* (Physalinae), occurring in a discernable physaloid clade in an unresolved association with *Acnistus* and *Tubocapsicum* (Acnistinae) and basal to a large clade containing *Cuatresia*, *Iochroma*, *Dunalia*, *Saracha*, and *Vassobia* (Iochrominae); (5) support for the transfer of *Larnax hunzikeriana* to *Cuatresia* (Sawyer, 1999b); (6) a monophyletic *Deprea* associated with a *Brachistus/Witheringia* clade (Witheringinae).

To further clarify relationships between *Deprea* and *Larnax*, a cladistic analysis was run that included *Deprea*, *Larnax*, *Brachistus*, and *Witheringia*, with *Aureliana* defined as outgroup. This analysis recovered a completely resolved single most parsimonious tree (419 steps; CI = 0.282; RI = 0.497; Fig. 3) with little internal support. The relationships among *Deprea*, *Brachistus*, and *Witheringia* remained unchanged from previous results. *Larnax* species occurred in a grade. Support (> 50% bootstrap) was present for the associations of *L. parviflora* with *L. psilophyta*, *L. harlingiana* with *L. hawkesii*, *L. subtriflora* with *L. suffruticosa*, and *D. bitteriana* with *D. paneroi* (Fig. 3).

DISCUSSION

These analyses suggest monophyly of *Deprea* and support the transfer of *D. glabra* and *D. sylvarum* to *Larnax* (Sawyer, 2001). The monophyly of *Larnax* (Fig. 1) also is supported with the above transfer and that of *C. hunzikeriana* to *Cuatresia* (Sawyer, 1999b). There is no support for the merging of *Deprea* and *Larnax*. Six unambiguous synapomorphies define *Larnax* and *Deprea* and support the placement of *L. glabra* and *L. sylvarum* in *Larnax*. These characters are filament length (heterodynamous vs. equal in size in *Deprea*), filament adnation (≤ 1.8 mm vs. ≥ 2.5 mm in *Deprea*), filament base expansion (abruptly expanded vs. tapering in *Deprea*), anther length (heterodynamous vs. equal in size in *Deprea*), and pollen surface texture (scabrate or psilate vs. rugulate in *Deprea*). The expanded filament base is the only character that has been used previously to distinguish these genera (Barboza & Hunziker, 1994). The equivocal use of this trait for *L. glabra* and *L. sylvarum* is clarified by their placement within *Larnax* (Sawyer, 2001). Generally, corolla shape, an equivocal character in the Barboza and Hunziker study (1994), can be used to separate the genera if the species with the epithets *glabra* and *sylvarum* are treated as *Larnax*. *Larnax* then possesses campanulate-rotate corollas (vs. infundibular in *Deprea*). This is equally true for species that possess a long corolla tube (5–7 mm long) relative to the limb (5–9.7 mm long; tube to limb ratio of ~ 50%), such as *L. cuyacensis*, *L. sachapapa*, and *L. suffruticosa*. Likewise, *D. paneroi*, a species that has a relatively short corolla tube (4.0–5.5 mm long in females, 4.5–7.3 mm long in males; tube to limb ratio of ~ 50%), has an infundibular corolla.

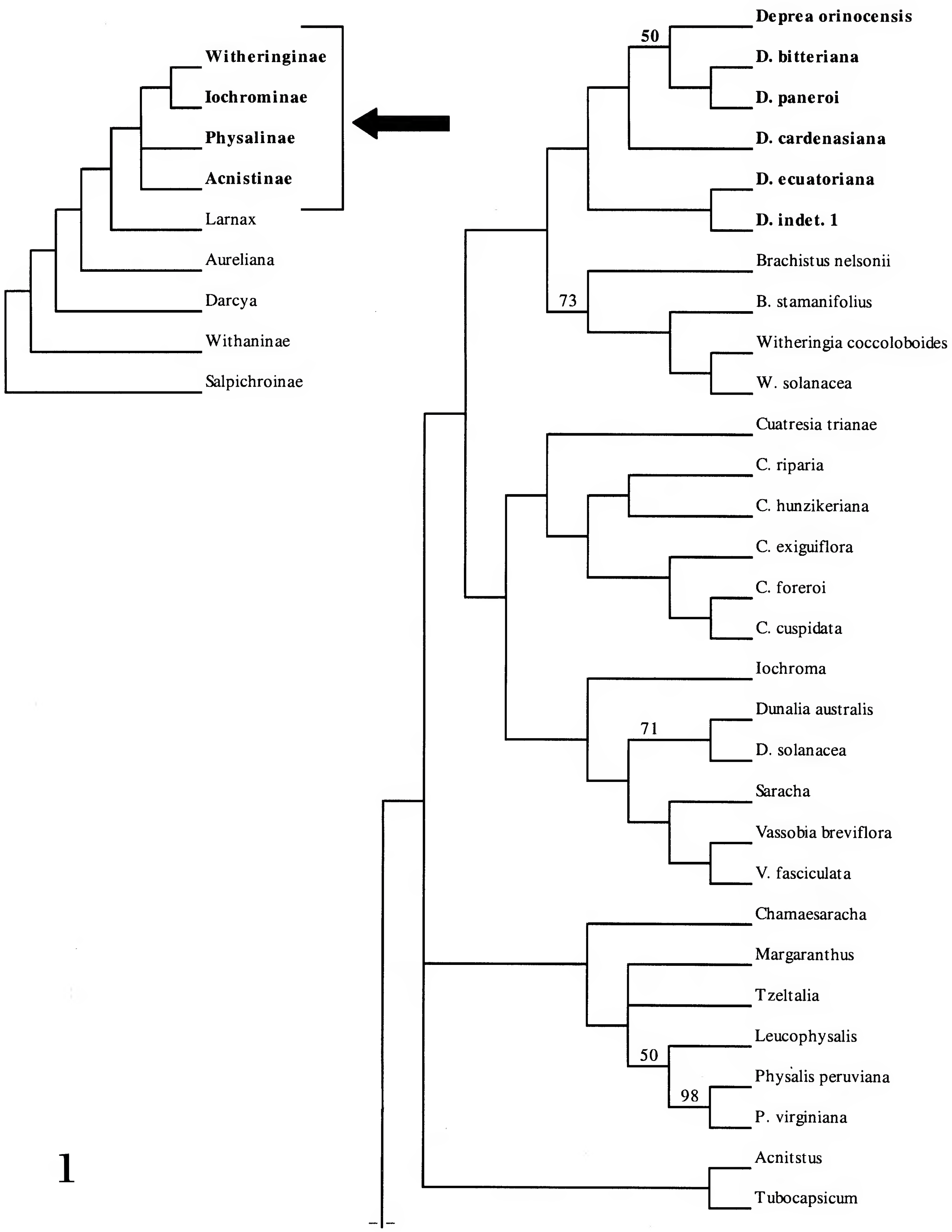
An as yet undescribed species of *Deprea*, endemic to the Sierra Nevada de Santa Marta in northern Colombia, occurs as sister to *D. ecuatoriana*, another species of limited distribution (southern Ecuador and northern Peru; Fig. 1). These two are the only *Deprea* species with fruiting calyces that are tightly appressed to the berries. The analysis (Fig. 1) also shows *D. orinocensis*, a species with a broad distributional range, having an ancestral association to the equally wide-ranging *D. bitteriana* and the Venezuelan endemic *D. paneroi*, a dioecious species (Sawyer & Anderson, 2000).

Evidence is lacking for a sister relationship of Old World *Withania* with New World *Deprea* or *Larnax* (Fig. 1) as suggested by Axelius (1996). Unlike either *Deprea* or *Larnax*, *Withania* inhabits semi-arid, lowland habitat, and, although *Withania* superficially resembles species of *Deprea*, especially in dried material (it does not resemble *Larnax*), distinct differences are apparent in living material (e.g., *Withania* species have a non-plagiotropic growth habit, fleshy vs. non-fleshy leaves with rounded vs. acute/apiculate leaf apices, and extrorse, ventri-fixed or ventri-basifixed vs. introrse, basifixed anthers). Unfortunately, the characters on which these differences are based are difficult to quantify. Convergent evolution may be an explanation for the morphological similarity of *Withania* and *Deprea. Withania*'s ancestral position in the topology (Fig. 2) is supported by its geographical distribution. *Withania* is primarily an African element, showing evidence of a Gondwanan radiation (Symon, 1991). This attaches a greater age to this taxon than to the montane South American taxa that appear to be derived and probably no older than 30 million years (Simpson, 1975, 1983). *Withania*'s sister association with *Athenaea* (Fig. 2) is interesting from a biogeographical viewpoint because *Athenaea* is found exclusively in eastern Brazil.

Likewise, a sister-taxon relationship of *Tzeltalia* with *Deprea* or *Larnax* (Estrada & Martínez, 1999) is unsupported by the results (Fig. 1). *Tzeltalia* nests within a group of physaloid genera (Fig. 1), which does not include *Deprea* or *Larnax*.

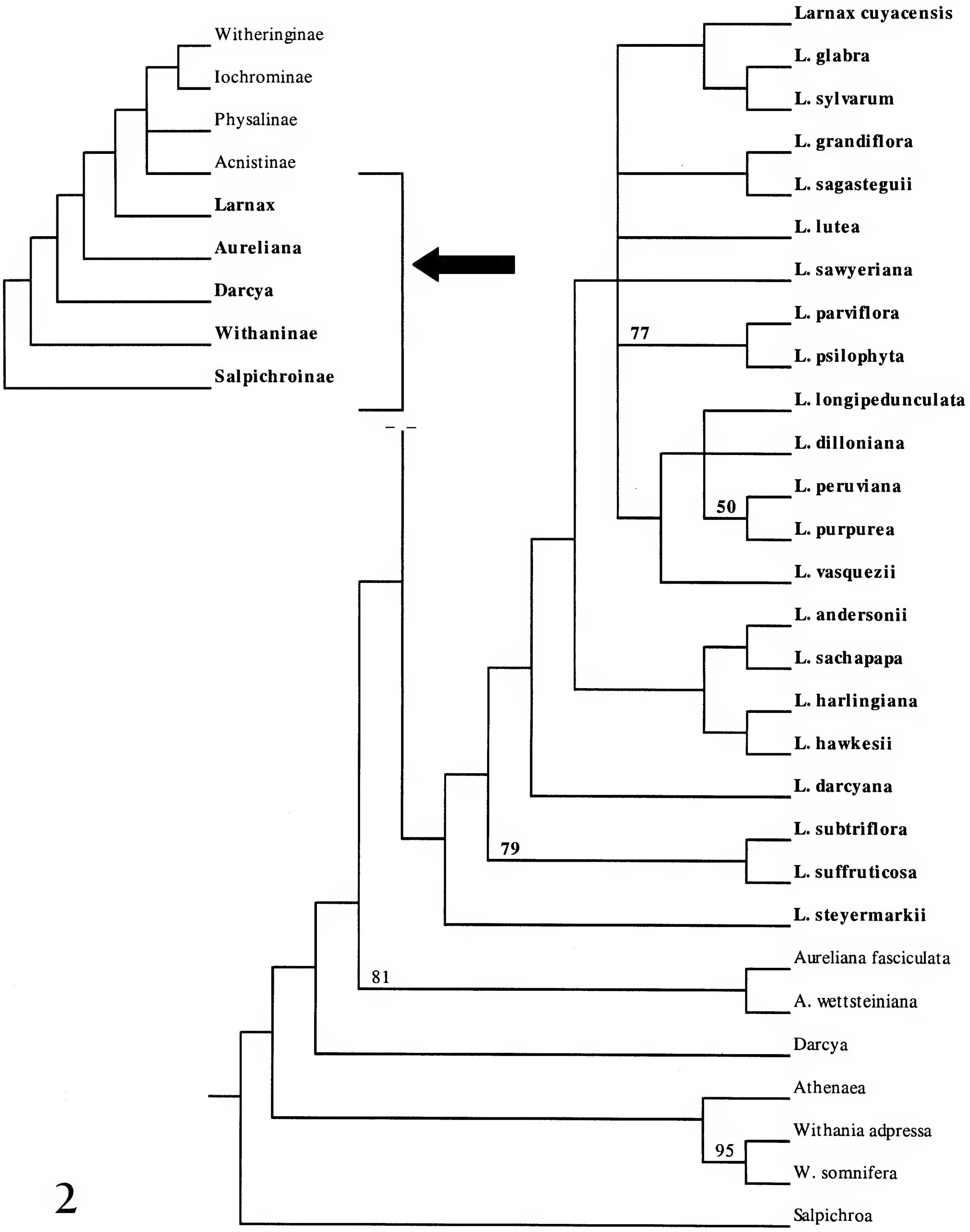
The sister-taxon relationship between *Larnax* and *Aureliana* is expected based on their very similar floral and vegetative morphology (e.g., both have campanulate corollas with < 50% tube-limb ratios and flaring corolla limbs, and both are shrubs with plagiotropic growth habit). *Larnax* is much more speciose than any other genus within Physaleae except *Physalis*. Of the 22 species making up the genus, 16 are found only in Peru or southern Ecuador. These species are ancestral to those found in northern Ecuador, Colombia, and Central America. *Larnax steyermarkii*, endemic to southern Ecuador, is at the base. This species is known from only two collections; the loss of habitat in that area, together with the inability of Sawyer to locate this species during fieldwork, indicate that it may be extirpated from its range. *Larnax darcyana*, known from a small area in south-central Colombia, is morphologically similar to *L. subtriflora* and *L. suffruticosa*, both found in northern Peru and southern Ecuador. *Larnax subtriflora* and *L. suffruticosa* occur as sister taxa; *L. subtriflora* has a widespread Peruvian distribution that overlaps with that of *L. suffruticosa* in northern Peru. The latter species is locally common, occurring also within the *Podocarpus* forests of southern Ecuador. Both species possess dendritic hairs. *Larnax suffruticosa* also contains irregular anthocyanic suffusions of purple in the corolla, unlike the purely yellow corolla of *L. subtriflora*.

Larnax harlingiana is a distinctive species with very long hairs, a relatively large green corolla with a reflexed limb, and an elliptic-fusiform fruiting calyx; this latter feature it shares with its sister taxon, *L. hawkesii*. In the same clade are the widely distributed *L. sachapapa*, the most morphologically variable *Larnax* species, and *L. andersonii*. Heterophylly among paired leaves occurs only in *L. andersonii* and *L. grandiflora*. Although their floral morphology is quite different (e.g., flowers of *L. grandiflora* are up to 2 cm long with glossy purple maculations between veins and with filaments adnate to the basal half of the corolla tube vs. flowers < 1 cm long in *L. andersonii* with dull purple maculations between veins only in sun plants and with filaments adnate to the basal 1/3 of the corolla tube), vegetatively they are nearly identical. The remaining *Larnax* species occur in a large clade with sister species *L. parviflora* and *L. psilophyta* at its base (Fig. 3). These are both small-flowered species (corollas typically < 5 mm long) with appressed fruiting calyces. This


Witheringinae
Iochrominae
Physalinae
Acnistinae
Larnax
Aureliana
Darcya
Withaninae
Salpichroinae
Deprea orinocensis
D. bitteriana
D. paneroi
D. cardenasiana
D. ecuatoriana
D. indet. 1
Brachistus nelsonii
B. stamanifolius
Witheringia coccoloboides
W. solanacea
Cuatresia trianae
C. riparia
C. hunzikeriana
C. exiguiflora
C. foreroi
C. cuspidata
Iochroma
Dunalia australis
D. solanacea
Saracha
Vassobia breviflora
V. fasciculata
Chamaesaracha
Margaranthus
Tzeltalia
Leucophysalis
Physalis peruviana
P. virginiana
Acnitstus
Tubocapsicum
50
73
71
50
98

1

Figures 1 and 2. Cladistic analysis of 20 genera in Physaleae based on morphological data (strict consensus of 166 most parsimonious trees; 819 steps; CI = 0.164; RI = 0.502). Bootstrap values greater than 50% appear above branches. Inset diagrams show proposed subtribes illustrated in each of Figure 1 and 2.


Witheringinae
Iochrominae
Physalinae
Acnistinae
Larnax
Aureliana
Darcya
Withaninae
Salpichroinae
Larnax cuyacensis
L. glabra
L. sylvarum
L. grandiflora
L. sagasteguii
L. lutea
L. sawyeriana
77
L. parviflora
L. psilophyta
L. longipedunculata
L. dilloniana
L. peruviana
50
L. purpurea
L. vasquezii
L. andersonii
L. sachapapa
L. harlingiana
L. hawkesii
L. darcyana
79
L. subtriflora
L. suffruticosa
L. steyermarkii
81
Aureliana fasciculata
A. wettsteiniana
Darcya
Athenaea
95
Withania adpressa
W. somnifera
Salpichroa

2

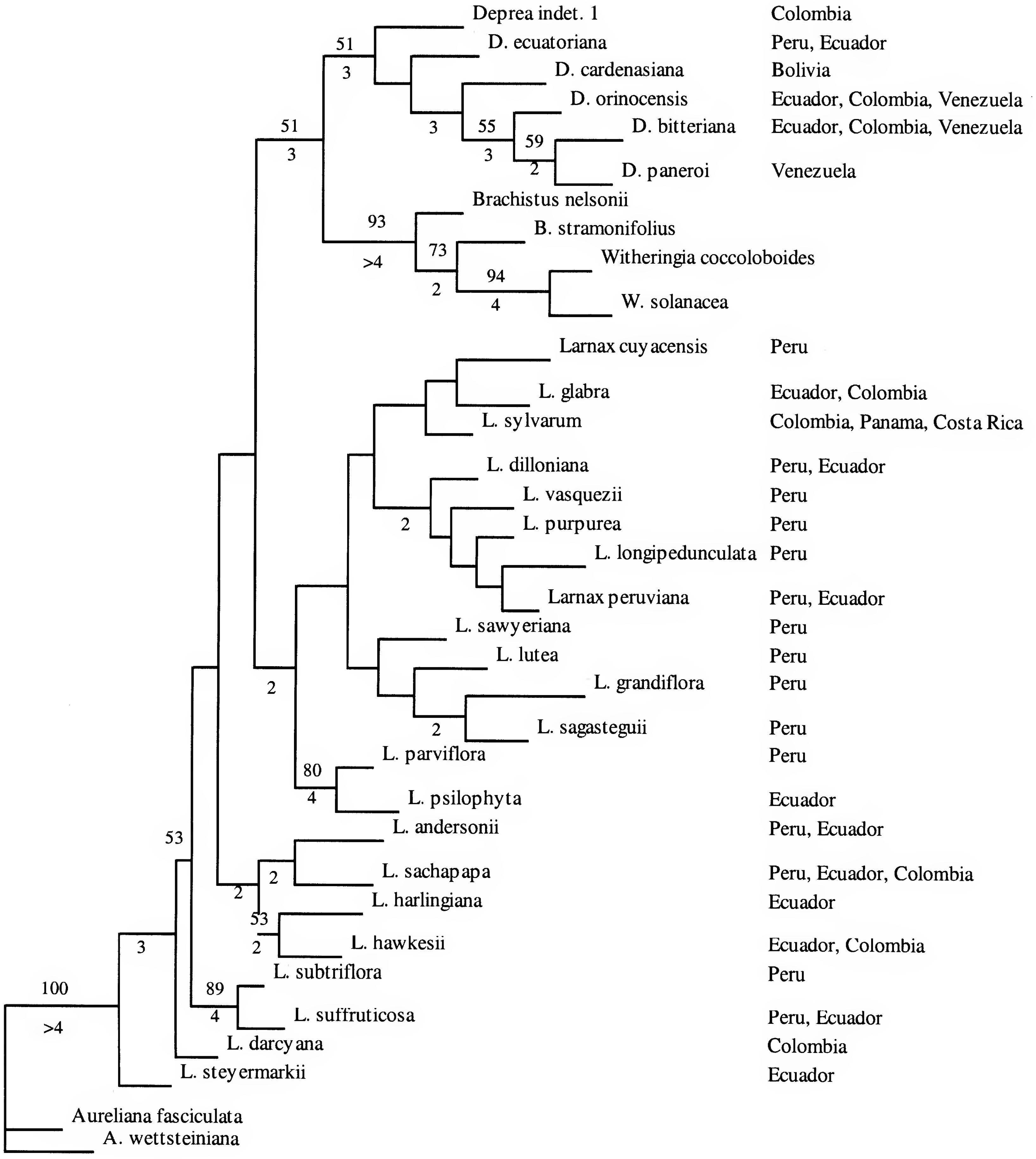

Deprea indet. 1
D. ecuatoriana
D. cardenasiana
D. orinocensis
D. bitteriana
D. paneroi
Brachistus nelsonii
B. stramonifolius
Witheringia coccoloboides
W. solanacea
Larnax cuyacensis
L. glabra
L. sylvarum
L. dilloniana
L. vasquezii
L. purpurea
L. longipedunculata
Larnax peruviana
L. sawyeriana
L. lutea
L. grandiflora
L. sagasteguii
L. parviflora
L. psilophyta
L. andersonii
L. sachapapa
L. harlingiana
L. hawkesii
L. subtriflora
L. suffruticosa
L. darcyana
L. steyermarkii
Aureliana fasciculata
A. wettsteiniana
Colombia
Peru, Ecuador
Bolivia
Ecuador, Colombia, Venezuela
Ecuador, Colombia, Venezuela
Venezuela
Peru
Ecuador, Colombia
Colombia, Panama, Costa Rica
Peru, Ecuador
Peru
Peru
Peru
Peru, Ecuador
Peru
Peru
Peru
Peru
Peru
Ecuador
Peru, Ecuador
Peru, Ecuador, Colombia
Ecuador
Ecuador, Colombia
Peru
Peru, Ecuador
Colombia
Ecuador
51
3
51
3
3
55
3
59
2
93
>4
73
2
94
4
2
2
2
80
4
53
2
2
53
2
3
89
4
100
>4

Figure 3. Cladistic analysis of ***Deprea*** and ***Larnax*** using morphology with ***Brachistus, Witheringia,*** and ***Aureliana*** included and ***Aureliana*** defined as outgroup (single most parsimonious tree; 419 steps; CI = 0.282; RI = 0.497). Bootstrap values greater than 50% are shown above the branches, Bremer decay index values greater than one below the branches. Geographic distributions for species of ***Deprea*** and ***Larnax*** are provided.

large clade consists of species from northern Peru (*L. psilophyta* is endemic to southern Ecuador) ancestral to species with northerly distributions. *Larnax sawyeriana* occurs as the ancestral species in an entirely Peruvian clade including *L. lutea*, *L. grandiflora*, and *L. sagasteguii* (Fig. 3). All of these species have appressed fruiting calyces (the fruiting calyx is unknown in *L. grandiflora*). The above clade is ancestral to a large clade with *L. cuyacensis*, a newly described species from northern Peru (Sawyer, 2001), *L. glabra*, and *L. sylvarum* at its base (Fig. 3). *Larnax cuyacensis*, a Peruvian endemic with an appressed fruiting calyx, closely resembles *L. glabra* and *L. sylvarum*. However, the calyces of *L. glabra* and *L. sylvarum* are inflated in fruit. The wide-ranging *L. glabra* overlaps with its sister species, *L. sylvarum*, in Colombia. These species are very similar morphologically, but *D. sylvarum* can be distinguished by the presence of hairs along the veins and branchlets (vs. glabrous) and by its smaller anthers and filaments (Sawyer, 2001). All species comprising the most derived clade of *Larnax* have inflated fruiting calyces. Among these, *L. dilloniana*, *L. peruviana*, and *L. purpurea* have plicate-ribbed calyces with invaginated bases that are characteristic of most *Physalis* species.

These results support Hunziker's (2000) belief that *Darcya spruceana* should be placed in its own genus. Results (see Fig. 1) show that this species is aligned with neither *Physalis* (Hunziker, 1961), *Brachistus* (D'Arcy, 1993b), nor *Chamaesaracha* (Hunziker, 1995). Instead, an ancestral relationship is suggested between this species and *Aureliana* and *Larnax* (Fig. 2). Whether these taxa should be placed together in a new subtribe or with *Athenaea* and *Withania* in the Withaninae is unclear, requiring more detailed analyses.

Based on these data, delimitation of a monophyletic physaloid clade containing taxa with the characteristic physaloid calyx is untenable. The evolution of an accrescent calyx that surrounds the fruit likely has occurred several times, viz., in nine of the ten species of *Withania* (absent in *W. qaraitica* A. G. Miller & A. J. Biagi), *Darcya spruceana*, *Larnax*, all genera closely aligned with *Physalis*, and two species of *Vassobia*. The topology suggests the loss of this calyx type in *Aureliana*, *Dunalia*, and *B. stramonifolius*. The more physaloid fruiting calyx, i.e., the pyriform, plicate-ribbed, inflated calyx with invaginated base, has evolved independently at least three times: in two species of *Withania* (*W. somnifera*, *W. obtusifolia*), most *Physalis* and their closest relatives, and three species of *Larnax* (*L. dilloniana*, *L. peruviana*, *L. purpurea*). Therefore, because neither *Withania* nor *Larnax* are closely related to *Physalis* (Figs. 1, 2), the taxonomic use of "physaloid taxa" either should be limited to circumscription of *Physalis* and its close relatives (excluding *Chamaesaracha*) or it should be discarded.

It is interesting to note that, based on character analysis of these results (Fig. 1, 2), the enveloping inflated accrescent calyx found in species of *Deprea*, *Cuatresia*, the physaloid genera, *Larnax*, and *Withania* appears to be derived from species possessing accrescent, enveloping calyces that are appressed to the fruit (not demonstrated here for *Withania*). Examples of this occur in *D. cardenasiana* and its derived associates, *C. riparia* var. *riparia*, *D. glabra* and *D. sylvarum*, the entire *Larnax* clade with *L. dilloniana* at its base (Fig. 3), and the physaloid genera derived from *Chamaesaracha*. In the case of *Witheringia*, although accrescence is retained, the calyx has lost the ability to envelop the berry.

Cuatresia is aligned in this analysis with a large clade of Central and South American genera that includes *Dunalia*, *Iochroma*, *Saracha*, and *Vassobia*, and should be placed with these genera in the Iochrominae. Formerly in *Larnax*, *C. hunzikeriana* is nested within *Cuatresia* (Fig. 1) as sister to *C. riparia* var. *riparia*. Its vegetative and reproductive morphology strongly supports the 1999 transfer (Sawyer, 1999b). Like other *Cuatresia*, and unlike *Larnax*, this species possesses heterophyllous leaves (vs. monophyllous in *Larnax*), peduncles to 2 cm long (vs. ≤ 0.5

mm) with pedicels developing in opposing pairs (vs. oblique development), induplicate-valvate corolla aestivation (vs. valvate), and ventrifixed anthers (vs. dorsifixed).

In addition, results (Fig. 1) do not support the varietal status allotted *Cuatresia riparia* and *C. cuspidata* (Hunziker, 1987). Hunziker (1977) originally had separated these taxa at the species level. This study supports his original hypothesis, basing the taxonomy on a few vegetative characters (e.g., mean petiole length ~ 10 mm in *C. riparia* vs. < 2 mm in *C. cuspidata*) and many reproductive characters (e.g., corolla length as a % of tube length 90–100% in *C. riparia* vs. < 50 % in *C. cuspidata*, filament length < 9 mm in *C. riparia* vs. > 12 mm in *C. cuspidata*, and anther length > 2.7 mm in *C. riparia* vs. < 2 mm in *C. cuspidata*). The diagnostic accrescent calyx of *C. riparia* clearly distinguishes this species from *C. cuspidata* (Hunziker, 1977, 1987).

A NOTE ON THE DISTRIBUTION OF *LARNAX* SPECIES

Northern Peru, the area of greatest diversity for *Larnax*, is a geologically complex region. The northern ranges of the Cordilleras Occidental and Oriental of Peru are separated from the western Cordillera and eastern Andes of Ecuador by the Huancabamba Deflection, a lowering in elevation of the Andes, and the upper Marañón Basin. The importance of the deflection in influencing evolutionary patterns is evidenced by the occurrence of several sibling pairs of *Larnax* species whose ranges are demarcated to the north and south by this barrier. These include *L. psilophyta* and *L. parviflora*, *L. suffruticosa* and *L. subtriflora*. Several species seem to be restricted to the area south of this barrier, viz., *L. grandiflora*, *L. purpurea*, *L. longipedunculata*, *L. lutea*, *L. sawyeriana*, and *L. vasquezii*. *Larnax subtriflora*, a species with a broad Peruvian range, *L. peruviana* and *L. andersonii*, both with a predominantly Ecuadorian distribution, are the only species whose ranges span the barrier. The geographic barrier is effective in delimiting vicariant patterns. However, it is not expected to be impenetrable because, based on personal observation, the fruits of the species in this group are likely dispersed by birds. Seeds, thus, may be moved quite easily across this and other orogenic barriers. However, unless repeated dispersal events occur into the same region and at least a few reciprocal dispersals emanate from it, the resultant reproductively isolated allopatric populations may follow independent evolutionary paths, leading ultimately to speciation events. Given the high occurrence of both endemism (half the species of *Larnax* and *Deprea* are endemics, i.e., they occur in restricted areas and nowhere else) and sympatry, especially in southern Ecuador and northern Peru, it may be more reasonable to attribute the distributional patterns to dispersal than to vicariance. The actions of vulcanism and human manipulation of the environment, and in some cases observed by Sawyer human use of fruit as food, also may have contributed to both movement and subsequent isolation of species, resulting in the observed high occurrence of endemism and restricted distributions.

In conclusion, results of cladistic analyses provide no justification for the merger of *Deprea* and *Larnax*. Morphological data provide phylogenetic evidence and six synapomorphies that *Deprea* and an enlarged, revised *Larnax*, including *L. glabra* and *L. sylvarum*, both formerly associated with *Deprea*, and *L. hunzikeriana* as transferred from *Cuatresia*, form monophyletic clades. Character analysis of fruiting calyx types suggests that inflated calyces have evolved from appressed calyces in many genera.

This study suggests *Brachistus* as the most probable sister genus to *Deprea* and *Aureliana* to *Larnax*. Further, due to their placement in the topology (Figs. 1, 2), *Withania* and *Tzeltalia* can be excluded from consideration as sister to either *Deprea* or *Larnax*.

The occurrence of a physaloid group as applied by Axelius (1996) united by a characteristic fruiting calyx is an artificial construct. Although several genera possess species with accrescent calyces that envelop the fruit, the typical physaloid calyx occurs only in *Physalis* and its close relatives, and in selected species of *Larnax* and *Withania* that do not appear to be closely related.

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APPENDIX 1.

Taxon by character matrix. See Table 5 for character descriptions and scoring. ( ) indicates characters represented by two or more character states in a species, interpreted as polymorphic.

	11111111112222222222	333333333344444	4444455	55555	55	56	66666666677	777	7777788
	12345678901234567890123456789	012345678901234	5678901	23456	78	90	12345678901	234	5678901
Acnistus arborescens	00100010001011010110110010020	000000002200000	0113110	10001	10	1?	00400010042	500	0000013
Athenaea picta	00100000211101111011011101020	000010113000001	1110120	11000	10	02	02010000030	001	02?0013
Aureliana fasciculata	00101101010001000010011101010	0002101031100(02)20110120		11000	10	11	00400100040	311	0031210
A. wettsteiniana	10111001011001100010001000010	0102101031100(02)10110120		10000	10	10	00400100041	111	0130?10
Brachistus nelsonii	10100000211001010010000111022	11021100210101(02)0110010		02001	10	00	00003100130	001	0000000
B. stramonifolius	00100010211001010010000110112	101210002101010	0010310	03000	00	01	00401100130	101	0001000
Chamaesaracha coronopus	00101000011001010010000010022	101110000931011	2113120	10010	10	1?	00003100030	100	0000310
Cuatresia exiguiflora	10112100100000000000010000010	000000002001010	1110020	02020	00	10	00003210033	?91	0210300

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C. foreroi

1010200000000000001100000011   10021100101100(02)1113000   02020   00   13   02000110043   ?91   0020310

C. riparia var. cuspidata

1010210100000000000010110001   100200002001010   1113000   02020   10   13   02400100043   ?91   0000200

C. riparia var. riparia

1011110010000000000010110001   100210002001010   1111010   02020   00   10   02003000122   501   0000310

C. trianae

0011111110000000000010010020   000100001001010   1113020   03020   00   1?   0?003100020   010   00?0??0

Darcya spruceana

0010001101110110001101100001   100100003011001   2113120   10010   21   1?   01002100040   51(01)0001300

Deprea orinocensis

1010100111100101101011011122   11020001211101(02)0012110   02000   10   1(12)02003201120   110   0000212

D. bitteriana

1010100110100100001001011101   010100102111031   0013110   02000   20   10   00003201121   310   0000312

D. cardenasiana

1000000111100101001001011002   100000102111000   0103200   02000   10   10   00003201111   110   00?0312

D. ecuatoriana

0000110011000101001001011001   100110013121010   0113110   02000   10   10   02103100141   410   01?0412

D. paneroi

1010100110100101001001011102   010100012111031   0011310   02001   10   10   02003200121   410   0010312

D. indet. sp. 1

1000100010100100001001011001   100010002131031   0013110   02000   10   10   02002100032   211   00?0412
```

APPENDIX 1 CONTINUED.

Dunalia australis

1110101000100101001001001 0010022 101100003001012 1103200 02100 00 1? 01401010024 510 0031313

D. solanacea

10100010111001000100110100122 010010003000010 1103200 02100 00 10 01401100024 210 0021313

Iochroma stenanthum

00100000110000010000011010010 000100002010110 1103300 02001 00 10 02003100024 300 00?1313

Larnax subtriflora

10100000111001010110100110110 000000003121010 011012(01)10000 11 00 0000310002(23)511 0000110

L. andersonii

10111000111001010110000110120 00000000093101(01)0110021 11001 21 01 01203100121 410 0000211

L. cuyacensis

10101001000000000000010110102 010011002111031 0111111 10000 11 11 00003101121 411 0010210

L. darcyana

10101001110001000010010110010 000000003121010 0110021 10001 11 01 00203100122 511 0000210

L. dilloniana

10100001110001000010010111010 000001002121021 0010221 10001 11 00 10303201101 210 0000210

L. glabra

10101101010000000000010110002 100000012111022 0111011 10000 11 10 02003201121 310 0000310

L. grandiflora

10111001101001010010000010021 110001010931001 0100221 10000 11 01 00?0??000?0 01? 0?????0

L. harlingiana

10001001111001010010000110020 000100103120020 0110321 11001 11 01 00103100121 411 01?0210

L. hawkesii

10100000111101010010010011010 000000002110022 0110121 11001 11 01 10103100121 011 01?0210

L. hunzikeriana

00112100100000000000010000002 110100001001010 1113010 02021 00 13 02003100022 101 0000200

L. longipedunculata

10101011110000000010010110000 000011001101021 0111121 11001 11 0? 00203201100 511 0000210

L. lutea

00101001110000000000010110012 110000012111010 0010121 10000 11 01 10002100101 310 0210010

L. parviflora

10102000110000000000010100002 100100003121010 0110321 11000 21 01 10003100140 511 0000410

L. peruviana

00101001110000000000010100000 00000101211100(01)0111121 11001 21 01 0030320110(03)510 0000310

L. psilophyta

10101100110000000000010000001 100101002121020 0110321 11000 11 03 00003100130 511 0000410

L. purpurea

10101100110000000000010100000 000000012111031 0110121 11001 11 01 00303201101 210 0000210

L. sachapapa

1010100011100101001001011002(01)100000012111000 011002(01)1100(01)11 1(12)01203201111 010 0200310

L. sagasteguii

10102000100000000010010110022 110201002111011 0110121 10000 11 00 00002110012 211 0000310

APPENDIX 1 CONTINUED.

L. sawyeriana	10001011111000010000010110012	110000013121011	0110121	10000	11	0?	11003101011	111	0000210
L. steyermarkii	00102001011001000010010110010	000010000931012	0110121	10000	21	00	01003100042	311	0020?10
L. suffruticosa	10101000111001010110100111111	1000000312101(02)	0110121	10000	11	01	01003100022	511	0000310
L. sylvarum	10101001010001000010010110012	100001002121022	0011121	10000	2(01)12		11003201131	411	0000310
L. vasquezii	10101001110000000000010100000	000001002121020	0110221	11001	11	01	10203100101	310	0210010
Leucophysalis grandiflora	001010100111011111011001010012	001200003011000	2113110	10000	00	0?	02013201020	000	0000000
Margaranthus solanaceus	00101000000001010010010010012	101100000931011	2113120	10010	20	0?	00003201110	200	0020310
Physalis peruviana	10101010011001010010001111012	001200000931011	2113100	00010	00	02	02303201100	000	0000010
P. virginiana	10101010011001010010011110012	001200000931011	2113110	00010	00	02	02303201100	000	0000010
Salpichroa tristis	101010001111011111011011010000	000000003021010	0103300	03000	10	1?	00001100040	010	0100410

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Saracha punctata

00101100110000010010010110022   101(012)1000200101(01)210300(01)0001000  13   02401000044   300   1001400

Tubocapsicum anomalum

00101011010000000000010100000   000000002020910   0112020   10000   20   1?   00400000043   590   0000310

Tzeltalia calidaria

00101001110000000000011110012   001100002011001   2110220   10010   00   1?   01203201100   110   0030310

Vassobia breviflora

01002100110000000000010010020   00010002001011   1011111   00000   01   00   02001110044   410   0001313

V. fasciculata

00102100110000011111111111122   001000002001001   1011001   10000   01   1?   00002100044   310   0001313

Withania adpressa

00102100101111111111111000122   101110002111020   0113320   13000   10   10   02003100140   401   0000403

W. somnifera

00001100111111111111111000122   001010003111020   0113320   13001   20   11   02303201121   200   0000313

Witheringia coccoloboides

10102000111001000010010110012   10110000210101(02)1013310   02001   00   0(12)00001010143   ?91   0000200

W. solanacea

10102000201001010010010010001   101100002001010   1011310   02001   20   01   01001000143   ?91   0000200
```

12

PALYNOLOGY AND SYSTEMATICS OF *PHYSALIS* (SOLANACEAE)

Janet R. Sullivan, Varsha P. Shah, and William Chissoe

Abstract. A complete description of the pollen of *Physalis* (Solanaceae) is given using information from light, scanning electron, and transmission electron microscopy. In addition, pollen features from 13 species and infraspecific taxa of *Physalis* were used to determine the congruence of palynological characteristics with other comparative data where available in the literature, such as macromorphology, secondary chemistry, interbreeding capabilities, and molecular data. The first level of comparison was made among species representing subgeneric categories based on morphology and chloroplast DNA data. The second level of comparison was made among species and infraspecific taxa within the subgeneric group characterized by dendroid-stelliform hairs (ser. *Stellatae* of Rydberg; sect. *Viscosae* of Martínez). The pollen morphology of all the species examined is relatively uniform, paralleling the great similarity within the genus in other floral features. *Physalis* has pollen grains that are subprolate in equatorial view and triangular with convex sides to round in polar view. The exine ornamentation is of minute spinules. The exine structure is characterized by a thick tectum, short columellae, the absence of a foot layer, and a well-developed endexine. The size range among taxa examined was 18.2–31.2 μm in polar diameter and 14.3–26.0 μm in equatorial diameter. Although some taxa in *Physalis* can be characterized by a combination of pollen features, the morphological and size variation do not consistently corroborate species relationships as determined by other types of analyses. Palynological features alone, therefore, are not particularly useful in distinguishing among taxa within *Physalis*. A broader approach, utilizing data from a combination of systematic techniques, is recommended.

Key words: *Physalis*, pollen morphology, SEM, Solanaceae, systematics, TEM.

Palynological investigations in the Solanaceae have been conducted at all levels in the taxonomic hierarchy, from broadly based surveys of genera and their tribal relationships (Basak, 1967; Murray & Eshbaugh, 1971; Gentry, 1979, 1986; Persson et al., 1994; Bernardello & Luján, 1997) to more comprehensive studies of species relationships and infraspecific taxa, particularly in the genus *Solanum* L. (Romanov, 1965; Anderson & Gensel, 1976; Gbile & Sowunmi, 1979), but also in the Salpiglossideae (Gentry, 1979). Before the 1980s, few pollen studies of the Solanaceae utilized scanning electron microscopy (SEM). However, SEM of pollen features is now used more commonly in combination with other types of data to determine relationships within the family (see especially Persson et al., 1994; Bernardello & Luján, 1997).

Basak (1967) distinguished eight different pollen types within the Solanaceae using light microscopy (LM). *Physalis* was included in the *Solanum* type, which was described as being 3-zonicolporate with distinctly lalongate os and a reticulate to subreticulate or psilate exine. In their LM survey of pollen in the subtribe Solaninae (of which *Physalis* is a member), Murray and Eshbaugh (1971) found the pollen morphology was "remarkably homogeneous." However, they concluded that many genera and species in the subtribe could be differentiated by combining morphological information with statistical data such as range, mean, variance, and standard deviation.

Gbile and Sowunmi (1979) determined that differences observed with LM in the size and shape of pollen grains and in the exine pattern were sufficient to distinguish species, subspecies, and varieties of some Nigerian members of the genus *Solanum*. In a study utilizing both SEM and LM, Anderson and Gensel (1976) found that differences in size and exine ornamentation served to distinguish species and series in *Solanum* sect. *Basarthrum*. Thus, morphological features and size of pollen may be useful in systematic studies on the generic level and, possibly, on the specific and subspecific levels in the Solanaceae.

Within the Solanaceae, *Physalis* L. is a large American genus comprising about 75 species (D'Arcy, 1991). The genus is characterized by pendent, yellow (in most species) flowers and an inflated fruiting calyx, which surrounds the berry in a bladder-like pouch; hence the generic name, which is Greek for "bladder." In 1896, Rydberg divided *Physalis* into subgeneric groups based on a combination of morphological features; some examples are annual or perennial habit, characteristics of the markings in the corolla throat (e.g., present or absent, brown or purple), shape of the fruiting calyx (e.g., 5-angled or terete, sunken at base or not), shape and relative length of the lobes of the flowering calyx, and character of the pubescence (e.g., simple or branched, glandular or not). In recent years, *Physalis* has been the focus of several systematic investigations in order to better understand patterns of karyology, hybridization, morphology, chemistry, and genetic variation within the genus (Menzel, 1951, 1957; Waterfall, 1958; Menzel, 1960; Waterfall, 1967; Hinton, 1970, 1975, 1976; Hudson, 1983; Sullivan, 1984a, 1984b, 1985; Seithe & Sullivan, 1990; Axelius,1992; Martínez, 1993; Estrada & Martínez, 1998; Martínez, 1999; Whitson, 2001). In 1999, Martínez provided a revised subgeneric classification based on a combination of the same morphological characteristics used by Rydberg and molecular characteristics (chloroplast DNA). Thus, the newer subgeneric classification takes into consideration our increased understanding of phylogenetic relationships within the genus. However, little is known about the variation in palynological features of *Physalis*, and their value in systematic analyses of the genus.

Murray and Eshbaugh (1971) examined pollen of four species of *Physalis* as part of their LM analysis of palynology of the Solaninae, but their purpose was to determine the significance of pollen features between, rather than within, genera. They characterized *Physalis* pollen as subprolate in equatorial view, semi-angular in polar view, with reticulate sculpturing, an ektexine that is thicker than the endexine, a small to intermediate polar area (Polar Area Index; Faegri & Iverson, 1964), and a somewhat inconspicuous vestibulum. They also found statistically significant differences in both polar and equatorial diameters among the four *Physalis* species they analyzed. Using LM and SEM, pollen was examined as part of a systematic study of the *Physalis viscosa* species complex (Sullivan, 1984a). Her results illustrated some qualitative and quantitative differences among pollen within the genus, as well as between the pollen of *Physalis* and *Quincula* (treated as *Physalis lobata* by some authors). In a study of "atypical" *Physalis*, Estrada and Martínez (1998) found that a suite of characteristics, which included pollen exine ornamentation, formed the basis for recognition of a distinct genus, *Tzeltalia*. They did not acetolyze pollen used in their study, nor did they indicate how many taxa were examined beyond the "atypical" ones (presumably their comparisons were made with the 10 *Physalis* species listed in their 1999 publication, although their focus in that study was on the atypical species in the genus and on generic relationships, rather than a general comparison among species within *Physalis*; Estrada & Martínez, 1999).

In this current study the pollen features of *Physalis* are described based on examination with LM, SEM, and transmission electron microscopy (TEM). In addition, the utility of palynology in systematic studies in *Physalis* is evaluated by comparing information on exine features and size of pollen with systematic studies based on other characteristics. First, comparisons were made at the level of subgeneric groupings of species: series within section *Euphysalis* from the morphology-based classification of Rydberg (1896) and sections within subgenus *Rydbergis* from the combined morphology and chloroplast DNA (cpDNA)-based classification of Martínez (1999; her subg. *Rydbergis* is comparable to Rydberg's sect. *Euphysalis*, see Table 1). Additional genetic information using two regions of nuclear DNA (*waxy* and ITS), newly available for some species (Whitson, 2001), was also considered at this first level of comparison. The second level of comparison was made among species and infraspecific taxa within the subgeneric group characterized by dendroid-stelliform hairs (ser. *Stellatae* of Rydberg, 1896; sect. *Viscosae* of Martínez, 1999). This species group has been studied in detail by Sullivan (1984a, 1984b, 1985) and by Seithe and Sullivan (1990), so several additional types of systematic data (e.g., morphology, flavonoid chemistry, interbreeding capabilities) were available for comparison.

MATERIALS AND METHODS

Pollen was examined from 13 species and infraspecific taxa of *Physalis* (Appendix 1). Originally, the taxa were chosen to provide one representative from each of the series in Rydberg's (1896) morphology-based classification of *Physalis* sect. *Euphysalis* (Table 1). Two of his series were not sampled because material was unavailable; thus, seven of his nine series are represented in this study. In addition, all of the members of Rydberg's series *Stellatae* were sampled because this species group had been the focus of extensive systematic research by Sullivan (1984a, 1984b, 1985) and by Seithe and Sullivan (1990), and so the morphology, flavonoid chemistry, and interbreeding capabilities are known in detail. After the pollen samples had been prepared, a new infrageneric classification of *Physalis* based on a combination of morphology and cpDNA data was proposed by Martínez (1999). The pollen samples in this current study represent five of the nine sections she proposed within subgenus *Rydbergis* (her subg. *Rydbergis* is comparable to Rydberg's sect. *Euphysalis*; see Table 1). Four new sections proposed by her to accommodate taxa from Mexico and Central America are not represented in this current study. Pollen samples were obtained from unopened anthers of greenhouse-grown plants (University of Oklahoma,

TABLE 1.

Physalis species sampled for this study, listed according to their classification in the morphology-based system of Rydberg (1896) and the combined morphology and chloroplast DNA-based system of Martínez (1999).

Rydberg (1896)	Martínez (1999)
Physalis sect. *Euphysalis*	*Physalis* subg. *Rydbergis*
I. Series *Pubescentes*	I. Section *Epeteiorhiza*
Physalis pubescens	*Physalis pubescens*
II. Series *Leptophyllae*	II. Section *Carpenteri*
Physalis carpenteri	*Physalis carpenteri*
III. Series *Angulatae*	III. Section *Angulatae*
Physalis angulata	*Physalis angulata*
IV. Series *Philadelphicae*	*Physalis philadelphica*
Physalis longifolia	IV. Section *Lanceolatae*
Physalis philadelphica	*Physalis heterophylla*
V. Series *Lanceolatae*	*Physalis longifolia*
Physalis pumila	*Physalis pumila*
VI. Series *Heterophyllae*	V. Section *Viscosae*
Physalis heterophylla	*Physalis angustifolia*
VII. Series *Stellatae* (species names here reflect the revised nomenclature of Sullivan, 1985)	*Physalis cinerascens*
Physalis angustifolia	*Physalis mollis*
Physalis cinerascens	*Physalis walteri*
Physalis mollis	VI. Section *Campanulatae* not sampled for this study
Physalis walteri	VII. Section *Coztomatae* not sampled for this study
VIII. Series *Versicolores* not sampled for this study	VIII. Section *Rydbergae* not sampled for this study
IX. Series *Crassifoliae* not sampled for this study	IX. Section *Tehuacanae* not sampled for this study

Norman) or from herbarium specimens. Vouchers are located in DUKE, FSU, MEXU, OKL, and USF. Samples were taken from one to nine populations of each taxon to represent different portions of the taxon's geographic range and the varying macromorphologies in the taxa chosen.

Pollen was acetolyzed according to the procedure given in Erdtman (1969) and filtered through a fine wire mesh to exclude undegraded anther tissue. A small portion of one sample population of each taxon was critical-point-dried using a Pelco Model H Critical Point Drying Unit and mounted in rubber cement on an aluminum stub for SEM. The stubs were coated with gold and stored in a dessicator until they were examined with an ETEC Autoscan. The remainder of each acetolyzed pollen sample was mounted on a glass slide in glycerine jelly for measurement with LM. For all collections, 20 measurements were made of the polar diameter (P) and of the equatorial diameter (E), and the P/E ratio was calculated.

Pollen of *Physalis cinerascens* and *P. pubescens* was also examined with TEM. For TEM, acetolyzed pollen was stained with 0.125% osmium tetroxide (OsO_4) and 0.5% uranyl acetate and embedded in epon and araldite (Skvarla, 1966). Thin sections were stained with uranyl acetate and lead citrate and were examined with a Philips model 200 TEM.

RESULTS

Pollen of all the species examined is similar in overall size, shape, and exine ornamentation, although some differences among species can be seen in these features (Table 2, Figs. 1 and 2). Pollen of *Physalis* is subprolate (Fig. 1A), and sub-circular to convex-triangular (Fig. 1B–D). The apocolpium is 0.2–0.4 diameter of the grain in polar view (Fig. 1B–D).

Physalis, Table 2, Figures 1 and 2.

Pollen tricolporate. Equatorial diameter 14.3–26 µm; polar diameter 18.2–31.2 µm; P/E

TABLE 2.

Size range, sample mean, and standard deviation in polar (P) and equatorial (E) diameter, and P/E ratio for *Physalis* specimens examined. Numbers represent the combined data for all sample populations of each species listed in Table 1. Twenty pollen grains from each population were measured in both polar and equatorial views. P/E ratios have been rounded off to the nearest 0.1. For simplicity, taxa are listed by series according to the classification of Rydberg (1896). For comparison, see the subgeneric classification of Martínez (1999) and Table 1 of this paper.

	Polar diameter (µm)			Equatorial diameter (µm)			
Taxon	Range	$\overline{X}$	S.D.	Range	$\overline{X}$	S.D.	P/E
Series *Angulatae*							
P. angulata	20.8–29.9	24.5	2.76	16.9–26.0	21.3	2.33	1.16
Series *Heterophyllae*							
P. heterophylla	20.8–26.0	23.6	1.37	18.2–20.8	19.0	1.02	1.24
Series *Lanceolatae*							
P. pumila	22.1–28.6	24.9	1.10	16.9–20.8	19.0	1.35	1.31
Series *Leptophyllae*							
P. carpenteri	20.8–24.7	23.1	0.82	15.6–20.8	18.5	1.29	1.25
Series *Philadelphicae*							
P. longifolia	20.8–26.0	23.0	1.48	15.6–18.2	17.1	1.14	1.34
P. philadelphica	23.4–31.2	26.4	1.89	15.6–20.8	18.4	1.06	1.44
Series *Pubescentes*							
P. pubescens	26.0–31.2	27.6	1.45	20.8–23.4	21.7	1.20	1.27
Series *Stellatae*							
P. angustifolia	20.8–27.3	24.3	1.51	18.2–23.4	19.9	1.37	1.22
P. cinerascens							
var. *cinerascens*	18.2–26.0	21.8	1.96	15.6–22.1	18.3	1.34	1.20
var. *spathulaefolia*	18.2–27.3	22.0	2.16	14.3–20.8	17.3	1.50	1.27
P. mollis							
var. *mollis*	20.8–28.6	24.2	1.94	15.6–23.4	19.6	1.35	1.23
var. *variovestita*	20.8–26.0	23.9	1.76	18.2–22.1	19.4	1.33	1.23
P. walteri	20.8–29.9	25.3	1.94	18.2–26.0	21.2	1.89	1.19

ratio 1.16–1.44. Grain in equatorial view subprolate. Grain in polar view sub-circular to triangular with slightly convex sides and ektexine protruding in the region of the endoaperture. Colpus extending almost the entire length of the grain; membrane psilate (Fig. 1E) to crustate (Fig. 1F); the endoaperture lalongate. Exine ornamentation of minute, rounded (Fig. 2A), or sharp spinules of varying degrees of density; spinules may be interspersed with minute, irregularly shaped granules (Fig. 2B). Tectum thick, becoming slightly thinner near the colpi; traversed by numerous fine, vertical channels (Fig. 2C, D). Columellae short, thick or thin, unbranched; some wider at their bases but footlayer absent. Endexine thick near the colpi, thick and lamellate near the endoapertures, and thin and uniform elsewhere.

Distinguishing features of each *Physalis* species examined are listed below. Species are listed alphabetically, for simplicity. Subgeneric classification according to Rydberg (1896) and Martínez (1999) is given for each (see also Table 1 for a comparison of the two classifications). Size ranges and P/E ratios are given in Table 2.

(A) *Physalis angulata* L. (ser. *Angulatae* of Rydberg; sect. *Angulatae* of Martínez)—Ektexine protrusions over the endoapertures

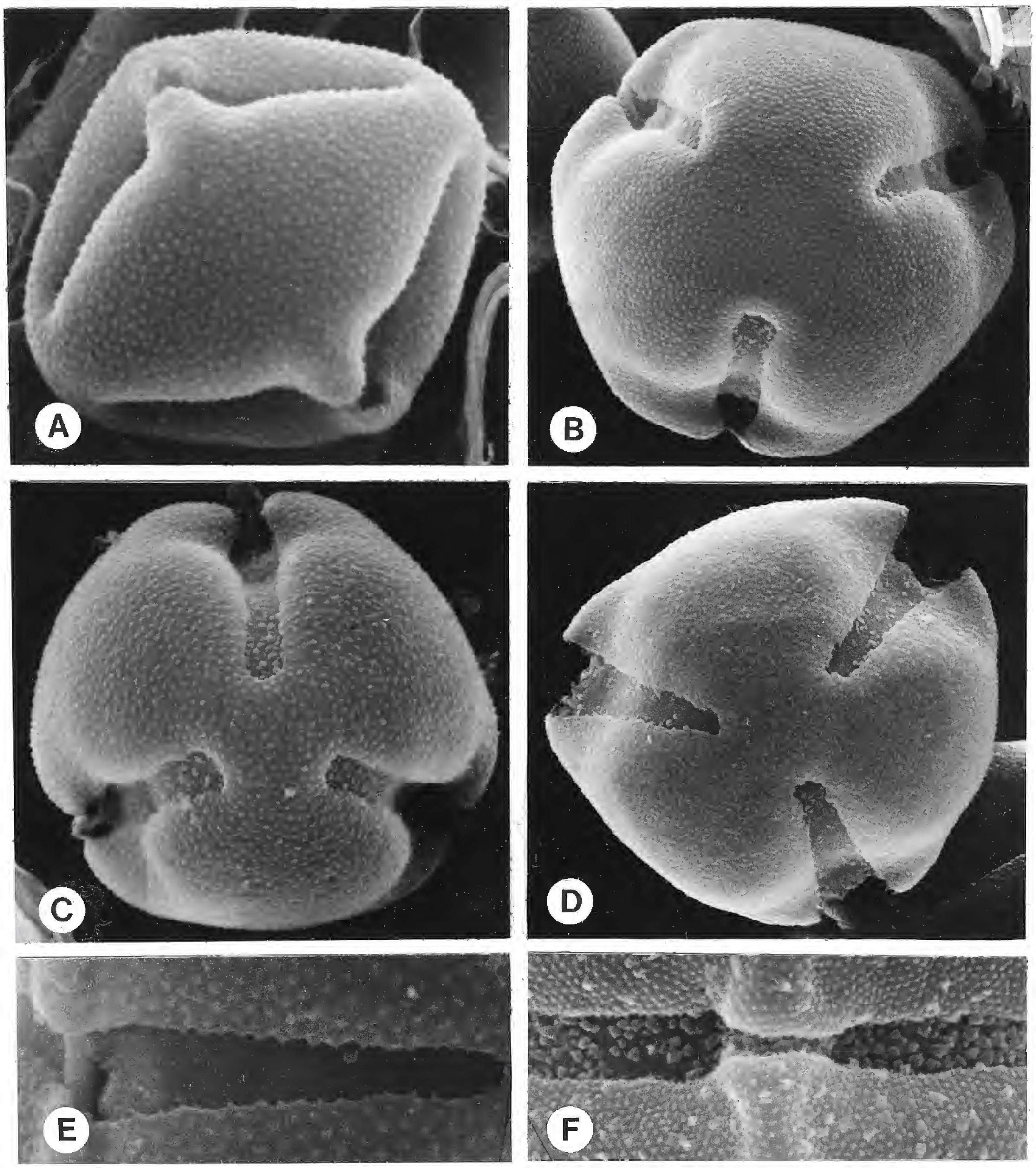

Figure 1. SEM of ***Physalis*** pollen. —A. ***P. carpenteri***, illustrating subprolate shape in equatorial view; × 4200. —B. ***P. cinerascens***, illustrating rounded ektexine protrusions extending over the colpi; × 4160. —C. ***P. walteri***, illustrating round shape in polar view; × 3675. —D. ***P. heterophylla***, illustrating triangular shape with convex sides in polar view and ektexine protrusions not extending over the colpi; × 3600. —E. ***P. philadelphica***, high magnification of the colpus illustrating psilate membrane; × 7000. —F. ***P. cinerascens***, high magnification of the colpus illustrating crustate membrane; × 6000.

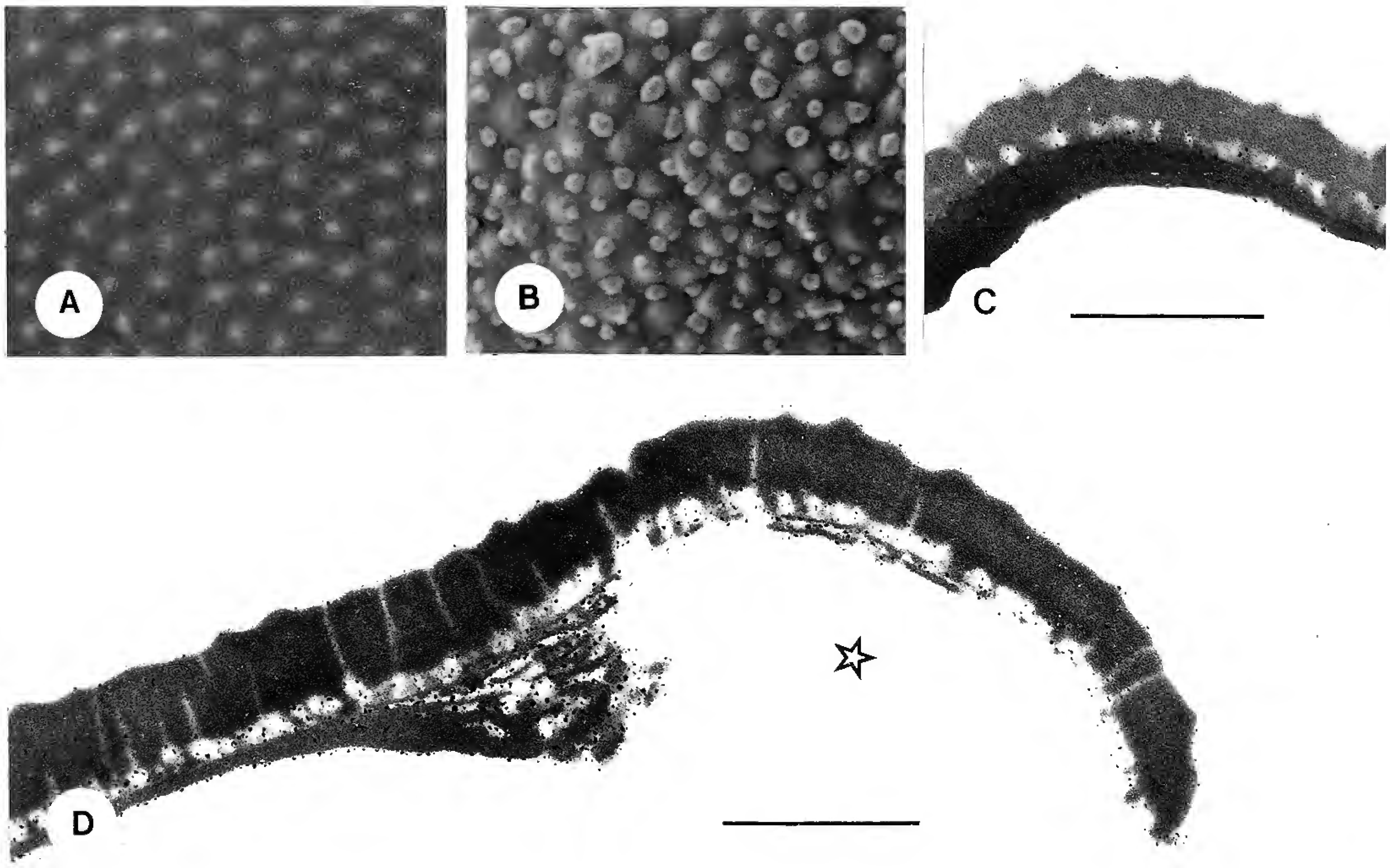

Figure 2. SEM and TEM of ***Physalis*** pollen. Bars on TEM photos equal 1 µm. —A. ***P. cinerascens***, high magnification of exine with rounded spinules; × 15,000. —B. ***P. pubescens***, high magnification of exine with rounded spinules interspersed with irregularly shaped granules; × 15,000. —C. ***P. cinerascens***, section passing through a portion of a mesocolpium near a colpus (left) but not near an endoaperture. Here the endexine becomes thicker but is not lamellated; × 19,600. —D. ***P. pubescens***, section passing through an endoaperture (star) and the adjacent mesocolpium. The tectum is very thick and uniform and has fine vertical channels. Short, thin, unbranched columellae are supported by a thin endexine that becomes thick and lamellated in the aperture region. Footlayer is absent. The ektexine extends over the endoaperture. × 19,600.

rounded and extending over the colpi. Colpus membrane granulate. Exine ornamentation of sharp-pointed spinules.

(B) *Physalis angustifolia* Nutt. (ser. *Stellatae* of Rydberg; sect. *Viscosae* of Martínez)—Ektexine protrusions over the endoapertures angular and not extending over the colpi. Colpus membranes granulate. Exine ornamentation of rounded spinules.

(C) *Physalis carpenteri* Rydb. (ser. *Leptophyllae* of Rydberg; sect. *Carpenteri* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending partially over the colpi. Colpus membranes sparsely granulate. Exine ornamentation of sharp-pointed spinules.

(D) *Physalis cinerascens* (Dunal) A. S. Hitchc. var. *cinerascens* and var. *spathulaefolia* (Torr.) J. R. Sullivan (ser. *Stellatae* of Rydberg; sect. *Viscosae* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending partially over the colpi. Colpus membrane granulate to crustate. Exine ornamentation of rounded spinules, in some populations these interspersed with small, irregularly shaped granules.

(E) *Physalis heterophylla* Nees (ser. *Heterophyllae* of Rydberg; sect. *Lanceolatae* of Martínez)—Extexine protrusions over the endoapertures angular and not extending over the colpi (Fig. 1D). Colpus membrane sparsely granulate. Exine ornamentation of only slightly raised, rounded spinules.

(F) *Physalis longifolia* Nutt. var. *longifolia* (ser. *Philadelphicae* of Rydberg; sect. *Lanceolatae* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending over the colpi. Colpus membrane crustate. Exine ornamentation of rounded spinules.

(G) *Physalis mollis* Nutt. var. *mollis* and var. *variovestita* (Waterf.) J. R. Sullivan (ser. *Stellatae* of Rydberg; sect. *Viscosae* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending partially over the colpi. Colpus membranes granulate. Exine ornamentation of rounded spinules.

(H) *Physalis philadelphica* Lam. (ser. *Philadelphicae* of Rydberg; sect. *Angulatae* of Martínez)—Ektexine protrusions over the endoapertures angular and not extending over the colpi. Colpus membrane psilate. Exine ornamentation of only slightly raised, rounded spinules.

(I) *Physalis pubescens* L. (ser. *Pubescentes* of Rydberg; sect. *Epeteiorhiza* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending over the colpi (Fig. 1B, C). Colpus membrane granulate. Exine ornamentation of only slightly raised, rounded spinules, interspersed with small, irregularly shaped granules.

(J) *Physalis pumila* Nutt. subsp. *pumila* (ser. *Lanceolatae* of Rydberg; sect. *Lanceolatae* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending over the colpi. Colpus membrane granulate. Exine ornamentation of rounded spinules.

(K) *Physalis walteri* Nutt. (ser. *Stellatae* of Rydberg; sect. *Viscosae* of Martínez)—Ektexine protrusions over the endoapertures rounded and extending partially over the colpi. Colpus membrane granulate. Exine ornamentation of rounded spinules.

DISCUSSION

Pollen morphology in *Physalis* is highly uniform, and there is a great amount of overlap among species examined in the size of grains. This is not surprising, in view of the great similarity among *Physalis* species in other floral characteristics (Rydberg, 1896; Menzel, 1951, 1957; Waterfall, 1958, 1967; Hinton, 1970, 1975, 1976; Hudson, 1983; Sullivan, 1984a, 1984b, 1985) and in pollination syndromes (Sullivan, 1984b). The flowers of all but a few species have shallowly lobed, campanulate, yellow corollas usually with five darker spots or smudges in the center and a mat of white hairs in the base of the throat where the stamens are inserted. The blossoms are pendent, and all species observed as part of a study of the pollination biology of *P. cinerascens* were pollinated by solitary bees in the genera *Perdita*, *Colletes*, and *Augochlorella*, which visited the flowers for nectar and pollen (Sullivan, 1984b).

Despite the relative uniformity in pollen shape and exine ornamentation in *Physalis*, the majority of representatives sampled for this study can be distinguished by a combination of differences in shape of the ektexine protrusions in the region of the endoaperture, size of the apocolpium, and exine ornamentation pattern. All of the *Physalis* species examined have protruding ektexine in the region of the endoaperture. However, in *P. angustifolia*, *P. heterophylla*, and *P. philadelphica* (each classified in a different subgeneric category according to both Rydberg, 1896, and Martínez, 1999; see Table 1) the protrusions are angular in polar view and do not extend over the colpi, while in the remaining species sampled the protrusions are rounded and extend at least partially over the colpi and pores. Size of the apocolpium is variable in the genus, from 0.2 to 0.4 of the grain diameter in polar view. Considerable variability occurs within species in this feature, as well.

There are also slight differences among *Physalis* species in exine ornamentation (for classification of each species mentioned within this general description of variation, the reader is referred to Table 1). Although the pollen of *Physalis* appears reticulate under the light microscope (as described by Murray & Eshbaugh, 1971), the higher resolution of the SEM reveals the exine of all species examined to be microspinulate. The minute spinules are rounded in most taxa, but sharp on *P. angulata* and *P. carpenteri*. The spinules are almost absent on *P. heterophylla*, such that the exine of this species appears only slightly roughened, perhaps comparable to the granular exine described by Estrada and Martínez (1998) for *P. arborescens* (classified in a different subgenus than the taxa described in the current study: subg. *Physalodendron*; Martínez, 1999). The pollen ornamentation of *P. philadelphica* and *P. pubescens* is similar to *P. heterophylla*, though both those species exhibit more widely spaced spinules that are only slightly raised. In addition, *P. pubescens* and some populations of *P. cinerascens* exhibit minute, irregularly shaped granules interspersed with the spinules. The occurrence of the granules is uniform in *P. pubescens* and irregular in *P. cinerascens*. The colpus membranes exhibited different degrees of granule density, from almost entirely smooth (psilate) in *P. philadelphica* to densely incrusted with granules (crustate) in *P. longifolia* and in one population of *P. cinerascens*.

In general, the variation seen among the *Physalis* taxa sampled is not great enough to allow for distinctions to be seen or correlations to be made among Rydberg's series nor with Martínez's sections. For example, the pollen grains of *P. heterophylla* (ser. *Heterophyllae* of Rydberg; sect. *Lanceolatae* of Martínez) and *P. philadelphica* (ser. *Philadelphicae* of Rydberg; sect. *Angulatae* of Martínez) are similar in exhibiting protrusions over the endoapertures that are angular and do not extend over the colpi, only slightly raised spinules on the exine, and a relatively smooth colpus membrane (sparsely granulate in the former species and psilate in the latter). The pollen of the two species also overlaps in size, although P/E ratios of the two are quite different (Table 2). The species are most likely distantly related, however, based on macromorphology, karyology, and molecular data (Rydberg, 1896; Waterfall, 1958, 1967; Martínez, 1999; Whitson, 2001). *Physalis philadelphica* is a taprooted annual from southern Mexico and Central America; it is glabrous to sparsely pubescent, has ovate to ovate-lanceolate leaves, short flowering and fruiting pedicels (3–6 mm and 3–11 mm, respectively), blue anthers that coil and twist upon dehiscence, and a purplish berry. *Physalis heterophylla* is a rhizomatous perennial species of temperate North America; it is villous and often glandular, has broadly ovate to suborbicular leaves, long flowering and fruiting pedicels (9–20 mm and 20–30 mm, respectively), yellow or only blue-tinged anthers that do not become coiled or twisted upon dehiscence, and a green berry.

Physalis heterophylla is considered to be closely related to the members of Rydberg's series *Lanceolatae* based on chromosome morphology, crossing behavior, and macromorphological features (Menzel, 1951; see also appendices in Sullivan, 1984a). In fact, Martínez (1999) combined Rydberg's series *Heterophyllae* and *Lanceolatae* in her section *Lanceolatae* based on a combination of morphological and cpDNA features (see comparison in Table 1). Martínez characterized her section *Lanceolatae* as being perennial herbs of the United States and Mexico with branching or simple hairs with an ornamented secondary surface, solitary flowers with yellow, rotate corollas with five spots in the throat, and terete fruiting calyces. Likewise, Whitson's (2001) nuclear DNA data supported a close phylogenetic relationship among the taxa she sampled from Martínez's section *Lanceolatae* (an exception being that her two-gene phylogeny using *waxy* and ITS shows *P. pumila* to be more closely related to the taxa in Martínez's sect. *Viscosae*; Rydberg's ser. *Stellatae*). Pollen morphology for the taxa in Martínez's *Lanceolatae* shows *P. pumila* and *P. longifolia* to be similar in having rounded ektexine protrusions over the endoapertures that extend over the colpi and an exine ornamentation of rounded spinules, but they differ from *P. heterophylla* in both of these features (*P. heterophylla* has angular protrusions that do not extend over the colpi and an exine ornamentation of only slightly raised, rounded spinules). Thus, the pollen morphology does not support the inclusion of *P. heterophylla* in the *Lanceolatae* as proposed by Martínez (1999) and supported by the data of Whitson (2001). Pollen morphology provides some support for Whitson's two-gene phylogeny (2001), which shows *P. pumila* to be more closely related to the members of section *Viscosae* of Martínez (ser. *Stellatae* of Rydberg). *Physalis pumila* is similar to three of the four members of section *Viscosae* in having rounded ektexine protrusions, a granular colpus membrane, and an exine with rounded spinules. The relationship of *P. pumila* to the members of section *Viscosae* is discussed in more detail below.

Another interesting contradiction involves *Physalis pubescens*, *P. angulata*, and *P. philadelphica*. These three species were classified in different series by Rydberg (1896; see Table 1). Martínez (1999) combined two of Rydberg's series such that *P. angulata* and *P. philadelphica* are both classified in her section *Angulatae*, based on cpDNA and morphology (she characterized the section as being annual or perennial herbs from the U.S., Mexico, and Central America with simple hairs or glabrous, flowers solitary with rotate or urceolate corollas, yellow or purple, with maculations that are absent or not strongly contrasting, and with terete fruiting calyces). This grouping is not supported by pollen morphology: *Physalis angulata* has rounded protrusions over the endoaperture that extend over the colpi, a granulate colpus membrane, and an exine ornamentation of sharp-pointed spinules, while *P. philadelphica* has angular protrusions that do not extend over the colpi, a psilate colpus membrane, and an exine of only slightly raised, rounded spinules. The recent two-gene phylogeny of Whitson (2001) also does not show a close relationship between these two species. In contrast, Whitson shows a close relationship between *P. angulata* and *P. pubescens*; this similarity is mirrored by pollen morphology, but not by the combination of morphology and cpDNA data (Martínez, 1999; Table 1). *Physalis pubescens* is similar to the members of section *Angulatae* except that it sometimes has glandular hairs and has a strongly 5-angled fruiting calyx. Clearly, we still have much to learn about phylogenetic relationships within *Physalis*, and pollen morphology may serve as corroborating evidence in some cases.

Physalis ser. *Stellatae* (or sect. *Viscosae*) has been found to be a distinct, although closely related, monophyletic group within the genus based on all types of data (Menzel, 1951;

Sullivan, 1984a, 1985; Seithe & Sullivan, 1990; Martínez, 1999; Whitson, 2001). The members of the group can be characterized as being perennials from the U.S., Mexico, and South America with a distinctive type of branched hair (dendroid-stelliform, see Seithe & Sullivan, 1990), a rotate yellow corolla with five contrasting maculations, and terete fruiting calyces. This study illustrates that there is variation in pollen morphology among species in the series/section, as well as variation within the species. For example, at the species level, *P. angustifolia* is the only member of the group that has angular ektexine protrusions over the endoaperture that do not extend over the colpi; the other three species have rounded protrusions that extend partially over the colpi. All four species have a granulate colpus membrane (or crustate in some populations of *P. cinerascens*) and an exine ornamentation of rounded spinules (in some populations of *P. cinerascens* these are interspersed with small, irregularly shaped granules). Thus, some populations of *P. cinerascens*, *P. mollis*, and *P. walteri* are indistinguishable based on pollen features alone. We found some variation within species in this series/section as well: both granulate and crustate colpus membrane types occurred in the populations of *Physalis cinerascens* examined, and this species and *P. walteri* exhibited considerable variability in the size of grains (Table 2). The four species in this series/section can be distinguished morphologically based on such features as pubescence characters (e.g., distribution of hair types, presence or absence of glands), leaf shape, features of the corolla (e.g., limb reflexed or not, maculations distinct or not), and anther characteristics.

Although each of the species examined is somewhat distinctive in possessing a particular combination of characters, the morphological and size variation alone was not great enough to provide insight into problematic relationships in the species examined. For example, as part of a systematic study of the *Physalis viscosa* species complex (ser. *Stellatae*; sect. *Viscosae*), Sullivan (1984a, 1985) noted some degree of similarity (in macromorphology, flavonoid chemistry, and a low degree of cross-compatibility) between the members of the species complex and *Physalis pumila* (series/section *Lanceolatae*). Subsequent study of hair morphology and development (Seithe & Sullivan, 1990) showed that the trichomes of *P. pumila* also are more similar to those of series *Stellatae* (sect. *Viscosae*) than series/section *Lanceolatae*. Whitson's nuclear DNA data (2001) illustrate similar affinities to those shown by pollen morphology. While members of both series *Stellatae* (sect. *Viscosae*) and series/section *Lanceolatae* have pollen exine ornamentation of rounded spinules, unlike any of the other taxa examined, other pollen morphological and size features show a conflicting pattern of similarities and differences among these taxa. *Physalis pumila* is more similar to the other species examined in Rydberg's series *Lanceolatae* (Table 1) in the character of the ektexine protrusions, P/E ratio, and size, though there is considerable overlap in the size of grains in the populations sampled. Thus, based on pollen features alone, it would be difficult to determine whether *P. pumila* has closer affinities to Rydberg's series *Lanceolatae* or his series *Stellatae.*

The overall uniformity of pollen in the genus is consistent with the high degree of similarity among *Physalis* species in other floral features. The majority of species in this genus have solitary, pendent, yellow flowers, usually with a mat of white hairs and dark maculations in the corolla throat. These floral similarities result in a similar pollination syndrome (pollination by solitary bees foraging for nectar and pollen) for the species observed (Sullivan, 1984b). Therefore, the uniformity in pollen morphology and size is not surprising.

Based on the comparisons among *Physalis* species within series *Stellatae* (sect. *Viscosae*) and among representative species from the other subgeneric groups in the genus, it is determined that palynological features alone do not shed new light on relationships within the genus. Information on pollen morphology and size thus may be most useful as corroborative evidence in systematic studies in the Solanaceae (Persson et. al., 1994; Bernardello & Luján, 1997; Estrada & Martínez, 1998).

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APPENDIX 1

Physalis specimens used for pollen analysis. All specimens listed were examined using LM. Each specimen followed by an [S] was also examined with SEM; each followed by a [T] was also examined with TEM.

P. angulata L. U.S.A. **Oklahoma:** Muskogee Co., *Little 188* (OKL). **Texas:** McLennan Co., *York 46232* (OKL). MEXICO. **Tabasco:** *Sullivan & Laue 1239* (OKL), [S], [T].

P. angustifolia Nutt. U.S.A. **Alabama:** Baldwin Co., *Sullivan & Laue 1164* (OKL). **Florida:** Charlotte Co., *Sullivan & Laue 1191* (OKL); Collier Co., *Sullivan & Laue 1208* (OKL), [S]; Franklin Co., *Sullivan & Laue 1169* (OKL), [S]; Lee Co., *Sullivan & Laue 1198* (OKL). **Mississippi:** Hancock Co., *Sullivan & Laue 1152* (OKL).

P. carpenteri Rydb. U.S.A. **Florida:** Jackson Co., *Mitchell & Ramsey 1100* (USF), [S]; Liberty Co., *Godfrey 71493* (FSU); Wakulla Co., *Godfrey 64173* (FSU).

P. cinerascens (Dunal) A. S. Hitchcock var. *cinerascens.* U.S.A. **Louisiana:** Webster Par., *Sullivan & Laue 1131* (OKL). **Oklahoma:** Cleveland Co., *Sullivan 1044* (OKL), [S], [T]; Woods Co., *Sullivan et al. 1068* (OKL). MEXICO. **Veracruz:** *Sullivan & Laue 1234* (OKL), [S], *1235* (OKL); *Roe et al. 1290* (MEXU). **Yucatán:** *Sullivan & Laue 1249* (OKL)*, 1256* (OKL), [S], *1257* (OKL).

P. cinerascens (Dunal) A. S. Hitchcock var. *spathulaefolia* (Torr.) J. R. Sullivan. U.S.A. **Louisiana:** Cameron Par., *Sullivan & Laue 1007* (OKL). **Texas:** Aransas Co., *Sullivan et al. 1126* (OKL), [S]; Nueces Co., *Sullivan et al. 1127* (OKL).

P. heterophylla Nees. U.S.A. **Colorado:** Larimer Co., *Eskew 259* (OKL). **Iowa:** Story Co., *Jeffs s.n.* (OKL 77106). **Oklahoma:** Cleveland Co., *Sullivan 1040* (OKL), [S].

P. longifolia Nutt. U.S.A. **Oklahoma:** Woods Co., *Sullivan et al. 1062* (OKL), [S].

P. mollis Nutt. var. *mollis.* U.S.A. **Louisiana:** Caddo Par., *Sullivan & Laue 1128* (OKL). **Oklahoma:** Marshall Co., *Sullivan & Laue 1045* (OKL). **Texas:** DeWitt Co., *Sullivan et al. 1123* (OKL); Harris Co., *Sullivan & Laue 1000* (OKL), [S]; Robertson Co., *Sullivan & Starbuck 1226* (OKL), [S].

P. mollis Nutt. var. *variovestita* (Waterf.) J. R. Sullivan. U.S.A. **Texas:** Aransas Co., *Sullivan et al. 1125* (OKL), [S].

P. philadelphica Lam. U.S.A. **New York:** Thompkins Co., *Hoisington 340* (OKL), [S]. **Virginia:** Arlington Co., *Green & Schmitt 3689* (USF). **Washington, D.C.:** *Steele s.n.* (DUKE 22985).

P. pumila Nutt. U.S.A. **Missouri:** Jackson Co., *Bush 12452a* (OKL). **Oklahoma:** Muskogee Co., *Bebb 33902* (OKL); Oklahoma Co., *Waterfall 1949* (OKL), [S].

P. pubescens L. U.S.A. **Texas:** Robertson Co., *Sullivan & Starbuck 1227* (OKL), [S], [T].

P. walteri Nutt. U.S.A. **Florida:** Broward Co., *Sullivan & Laue 1211* (OKL); Dade Co., *Sullivan & Laue 1209* (OKL), [S], *1210* (OKL); Dixie Co., *Sullivan & Laue 1010* (OKL); Glades Co., *Sullivan & Laue 1203* (OKL), [S]; Nassau Co., *Sullivan & Laue 1183* (OKL); Pasco Co., *Sullivan & Laue 1032* (OKL). **North Carolina:** Pender Co., *Sullivan & Laue 1221* (OKL).

13

NECTAR SECRETION PATTERN AND REMOVAL EFFECTS IN ARGENTINE *LYCIUM* (SOLANACEAE)

Gabriel Bernardello and Leonardo Galetto

Abstract. Nectar secretion pattern and effects of nectar removal were compared in five Argentine species of *Lycium* (Solanaceae) from several phytogeographical regions with different floral morphologies and floral visitors. The studied species produced small amounts of nectar volume (< 5 mL). Nectar had a low sugar concentration when the flowers first opened (9–22%, except for the Patagonian *L. chilense* var. *filifolium* with 50%), but concentration quickly reached higher values (27.7–75.8%). In none of the species did the buds produce nectar. Nectar was mainly secreted during the first day of anthesis. An active nectar resorption period can be inferred during the last hours of the flower lifetime in *L. americanum*, *L. elongatum*, and *L. gilliesianum* due to a decrease in the content of the nectar sugars. *Lycium chilense* var. *filifolium* seems to follow the same trend, but this was difficult to confirm due to the small amount of nectar per flower. *Lycium vimineum* had an increase in the nectar sugar content at the end of the flower lifetime. All species continued to secrete nectar after removal. In *L. gilliesianum*, *L. elongatum*, and *L. americanum* the total amount of nectar secreted by flower sets subjected to removals was lower than control sets. The earlier the removal, the lower the total nectar secreted by a flower. On the other hand, there was an increase in nectar production in *L. vimineum* and *L. chilense* var. *filifolium*, but there were no significant differences between experimental and control sets. These results, together with data on two other species previously studied, indicated that nectar secretion pattern is conservative for the genus, but several patterns were detected as a result of removal on nectar production. None of them could, however, be drawn to particular habitats, flower structures, or pollinator guilds of the involved *Lycium* species.

Key words: Argentina, *Lycium,* nectar removal, nectar secretion pattern, Solanaceae.

Patterns of nectar production and effects of nectar removal on flowering plants have received little attention (e.g., Galetto & Bernardello, 1992; Torres & Galetto, 1998; Navarro, 1999; Galetto et al., 2000) compared with the chemical constituents of nectar (e.g., Stiles & Freeman, 1993; Van Wyk, 1993; Bernardello et al., 1999; Galetto & Bernardello, 2003). However, both processes are key for understanding the ecology of the plant-pollinator interaction. Studies on flowers and their animal visitors have assumed coevolutionary relationships between nectar traits and pollinator type. Nectar secretion pattern and effects of removal on nectar production show diverse patterns relative to the different guilds of pollinators that visit the flowers and with respect to the plant reproductive success (e.g., Feinsinger, 1978; Cruden et al., 1983; Galetto & Bernardello, 1992).

This general trend applies to the Solanaceae as well, a family of economic importance (D'Arcy, 1991). Several papers document the nectar composition of about 50 Solanaceae species from several genera (*Atropa*, *Browallia*, *Brunfelsia*, *Cestrum*, *Datura*, *Fabiana*, *Nicandra*, *Nicotiana*, *Petunia*, *Physalis*, *Salpiglossis*, *Schizanthus*, *Streptosolen*: Percival, 1961; *Streptosolen*: Shuel, 1961; *Markea*: Voss et al., 1980; *Acnistus*, *Witheringia*: Guerrant & Fieldler, 1981; *Nicotiana*: Hernández, 1981, Galetto, 1991, Bernardello et al., 2000; *Datura*: Cruden et al., 1983, Freeman & Worthington, 1985; *Cestrum*, *Datura*: Gottsberger et al., 1984; *Atropa*: Herrera, 1985; *Browallia*, *Cestrum*, *Cuatresia*, *Iochroma*: Bernardello et al., 1994). However, patterns of nectar production throughout the duration of a flower and the effect of nectar removal on production rates have only been exceptionally investigated in the family (e.g., *Streptosolen*: Shuel, 1961; *Nicotiana*, *Petunia*: Galetto & Bernardello, 1993; *Jaborosa*: Vesprini & Galetto, 2000).

Within the shrubby genus *Lycium* L. (Solanaceae, Solanoideae, Lycieae), 21 taxa have been studied for nectar composition (Bernardello, 1986a; Bernardello et al., 1995; Galetto & Bernardello, 1996; Galetto et al., 1998), but only two species and their hybrid have been examined in their nectar secretion pattern and removal effects (*L. cestroides* Schltdl., *L. ciliatum* Schltdl.; Galetto & Bernardello, 1996). This cosmopolitan genus contains about 80 woody species, which grow mainly in arid or semiarid environments (Bernardello, 1986b). Recent molecular cladistic analyses suggest that *Lycium* is not monophyletic, but includes the genus *Grabowskia* Schltdl. (Miller, 2002), another American member of the tribe (Bernardello, 1987). Most of the species (51) are confined to the American continent, with two centers of diversification: Arizona (U.S.A.) and Argentina (Hitchcock, 1932; Bernardello, 1987; Bernardello & Chiang Cabrera, 1998). The South American species in general, and the Argentine in particular, include all the flower types of the genus (from long tubular corollas with very short lobes to extremely short corollas with long lobes; Bernardello, 1987) and also the different insect visitors, which include Hymenoptera, Diptera, and Lepidoptera; only one species (*L. cestroides*) is visited by hummingbirds (Galetto et al., 1998).

The present study was undertaken to compare floral nectar secretion in five Argentine *Lycium*: *L. americanum* Jacq., *L. chilense* Miers ex Bertero var. *filifolium* (Miers) Bernardello, *L. elongatum* Miers, *L. gilliesianum* Miers, and *L. vimineum* Miers. The following questions were addressed for each species:

(1) What is the secretory pattern of nectar throughout the duration of a *Lycium* flower?

(2) What is the floral response to nectar removal?

(3) Are there differences in the nectar patterns according to the habitat, the type of visitors, or floral morphology?

MATERIALS AND METHODS

The populations studied in *Lycium* are vouchered in Table 1.

Lycium americanum is a widespread species that grows in xerophytic regions from the Caribbean to Argentina (Bernardello, 1986b). The flowers have an infundibuliform, white to lilac corolla, with middle-sized tube and long lobes (range: 5–8 mm and 2.5–4.5 mm, respectively), and exserted stamens. Its ovary has one inconspicuous green basal nectary (Bernardello, 1987). Insects reported as visitors (Galetto et al., 1998) include Diptera (Conopidae), Hymenoptera (Apidae), and Lepidoptera (Lycaenidae).

Lycium chilense var. *filifolium* is endemic to Chile and Argentina, where it is native in the Monte, Espinal, and Patagonia phytogeographical provinces (Bernardello, 1986b) that include arid and semiarid environments. These flowers have a white corolla with a very short tube and long spreading lobes (range: 2.5–4 mm and 3–5 mm, respectively). Stamens are much exserted with enlarged fringed filament bases. The ovary has a green inconspicuous nectary (Bernardello, 1987). Flies (Syrphidae) and bees (Halictidae) are regular visitors of these shrubs (Galetto et al., 1998).

Lycium elongatum is endemic to the Argentine Chaco (Bernardello, 1986b), a mesophytic region. Its flowers have a tubular lilac corolla with long tubes (8–10 mm), very short lobes (2–3 mm), and mostly inserted stamens. Bees (Apidae) are frequent visitors (Galetto et al., 1998).

Lycium gilliesianum is endemic to Argentina and inhabits the phytogeographic provinces of Patagonia, Monte, and Espinal (Bernardello, 1986b). The flowers have long narrow tubular corollas (10–15 mm) with very short lobes (1–2 mm) and included stamens. The ovary has a conspicuous red nectary at its base (Bernardello, 1987). Diurnal butterflies (Pieridae) and bees (Apidae) visit this species (Galetto et al., 1998).

Lycium vimineum is a hygrophilous shrub endemic to Argentina and Uruguay (Bernardello, 1986b). Its flowers resemble those of *L. americanum*, but are white with a conspicuous red nectary (Bernardello, 1987). These shrubs are mainly visited by nocturnal sphingid moths (Sphingidae), as well as by diurnal bees (Apidae), wasps (Vespoidea), and butterflies (Nymphalidae).

Floral longevity was determined in bagged flowers by following the flowers' development until the corollas began to wilt. Randomly chosen inflorescences in bud stage were bagged using paper bags to prevent pollinator visits. Individual buds were tagged for identification.

Nectar was extracted with capillary glass tubes without removing the flowers from the plant, avoiding damage to the nectaries. Two variables were immediately taken: volume (in mL) using graduated micropipettes and sugar concentration (%, mass/total mass) with a pocket refractometer (Atago, Japan). The amount of sugar produced was expressed in milligrams and was calculated after Kearns and Inouye (1993).

Nectar production was determined by using flower sets of 7 to 10 flowers each. To diminish interplant and temporal variability, flowers of the same age from different plants were included in each set and all the measurements were performed in the same period. When more than two flowers of the same individual were used for a set, we pooled these data using the mean of the plant sample for statistical analyses. The study period was extended across the flower lifetime as noted for each species (cf. Table 2). Data were taken once for each floral set allowing the nectar to accumulate until the timed nectar withdrawal. Net nectar production rate per hour was calculated as: mg of sugar produced between measurements/# of hours between them (mg h^{-1}), while net nectar resorption rate per hour as: mg of sugar resorbed between measurements/# of hours between them (mg h^{-1}).

To evaluate the effect of nectar removal on nectar production, nectar was removed and measured from the same flower repeatedly during the entire active secretion period. This period was very short and varied according to the species: ca. 24 h in *L. chilense*, ca. 32 h in *L. gilliesianum*, ca. 36 h in *L. vimineum* and *L. americanum*, and ca. 48 h in *L. elongatum*. Sets were subjected to a different number of removals according to the flower duration of the species. The general scheme (see Table 2) was: set 1 = 3 to 5 removals were performed starting from flower opening; set 2 = nectar was allowed to accumulate for 6–12 h, and then 2 to 4 removals were performed; set 3 = nectar was allowed to accumulate for 12–24 h, and then 1 to 3 removals were performed. In species with longer secretion periods (*L. vimineum*, *L. elongatum*, *L. americanum*), additional sets were used with the same scheme. In the control set (the older flower set not yet involved within the resorption period), nectar was allowed to accumulate during the entire secretion period and only one removal was performed at the end of the experiment.

Statistical tests were performed using methods described in Sokal and Rohlf (1995). All distributions were tested for randomness of nominal data (Runs test), homogeneity of variances (Levene test), and departures from normality (Kolmogorov-Smirnov for goodness of fit test). The effects of nectar removal in the total mg of sugar produced (log transformed +1) by each set of flowers were compared with one-way analysis of variance (ANOVA) and with the Bonferroni's post-hoc test for multiple comparisons among pairs of means.

RESULTS

NECTAR PRODUCTION

In none of the species did the buds produce nectar. As soon as a flower opened, nectar was secreted in low concentrations (Table 2): 9–22% (higher in *L. chilense* var. *filifolium* with 50%). Throughout the flower lifetime, nectar concentration reached higher values, according to the species (up to 75%, see Table 2). *Lycium americanum* showed a shorter concentration range: from 11.6% when the flower opened to 27.7% at the end of its lifetime (Table 2). Nectar volume secreted per flower is less than 5 mL in all species (Table 2).

During the first 1 to 2 hours of anthesis, flowers secreted less than 25% of the total nectar production. The one exception was *L. chilense* var. *filifolium*, where most nectar was produced in that period. *Lycium elongatum* and *L. gilliesianum* continuously secreted nectar from the time flowers opened. *Lycium americanum* and *L. vimineum* secreted nectar during the two days of their flower lifetime with a short cessation period.

After nectar secretion, an active nectar resorption period can be inferred during the last hours of the flower lifetime in *L. americanum*, *L. elongatum*, and *L. gilliesianum* due to a decrease in the mean content of the nectar sugars per flower (Table 2). *Lycium chilense* var. *filifolium* seems to follow the same trend, but this was difficult to confirm due to the small amount of nectar per flower. On the other hand, *Lycium vimineum* had an increase in the nectar sugar content at the end of the flower lifetime. Nectar secretion rates per hour showed values from 0.01 to 0.12 mg h^{-1} (all species) and nectar resorption rates per hour from -0.03 to -0.08 mg h^{-1} (*L. americanum*, *L. elongatum*, *L. gilliesianum*).

REMOVAL EFFECTS

According to our results, all five species continued to secrete nectar after removal (Table 2). However, in *Lycium gilliesianum*, *L. elongatum*, and *L. americanum* the mean total amount of nectar secreted per flower from sets subjected to removals was lower than control sets ($F_{[3,\,30]} = 7.51$, $P < 0.0008$; $F_{[3,\,12]} = 15.87$, $P < 0.0001$; $F_{[4,\,25]} = 4.39$, $P < 0.008$, respectively; see Table 2 for post-hoc test results). Untouched flowers that were within the nectar resorption period were excluded for statistical analyses (underlined data in Table 2). The earlier the removal, the lower the total nectar secreted by a flower, a particularly clear pattern in *L. elongatum* (Table 2). On the other hand, there was an increase in nectar production in *L. vimineum* and *L. chilense* var. *filifolium*, but there were no significant differences between experimental and control sets ($F_{[3,20]} = 2.78$, $P < 0.06$; $F_{[3,24]} = 1.48$; $P < 0.27$, respectively).

DISCUSSION

Nectar studies may give clues on the taxonomic affinities of the species concerned, and on the adaptation to the pollinators that visit the taxa, particularly when studying closely related species of a genus. The seven *Lycium* species analyzed up to now (Galetto & Bernardello, 1996: *L. ciliatum*, *L. cestroides*; this paper) include a wide range of floral morphologies, visitors, and habitats within the genus (see Material and Methods; Bernardello, 1986b, 1987; Galetto et al., 1998). Accordingly, we would expect differences in nectar sugar composition and in the nectar secretion pattern and effects of removal related to those factors; i.e., species with long or short corolla tubes, visited by different pollinator guilds, growing in arid or humid environments. In spite of this, nectar traits in *Lycium* showed a remarkable constancy. Effectively, 21 diverse *Lycium* taxa had a uniform nectar sugar composition (Galetto et al., 1998), and the nectar secretion pattern of the seven species studied up to now (Galetto & Bernardello, 1996; this paper) was comparable. In general, the flowers of these seven species produced small amounts of nectar, at low concentration when the flowers opened but then quickly concentrating. At the end of the flower lifetime there is an inferred period of active resorption for most species (*L. americanum*, *L. elongatum*, *L. gilliesianum*, *L. ciliatum*, *L. cestroides*).

On the other hand, there are differences among the *Lycium* species known in the effect of removal on their total nectar secretion. There are two main trends: (1) total production is not affected by removal in *L. vimineum*, as previously noted for *L. ciliatum* (Galetto & Bernardello, 1996), and (2) total production is inhibited by removal, as in *L. elongatum*, *L. gilliesianum*, and *L. americanum*. Only *L. cestroides* previously showed an increase in total nectar production after removal (Galetto & Bernardello, 1996). In addition, this species had the highest nectar volume secreted per flower (> 10 mL). This high nectar availability per flower in *L. cestroides* may be related to the fact that it is the only South American hummingbird-visited species of *Lycium* (Galetto et al., 1998).

The species where nectar production is unaffected by nectar removal occur in humid or arid habitats, are visited by bees, flies, or nocturnal sphingid moths, and have flowers with very short or medium-sized corolla tubes. In them, flowers have a fixed amount of nectar to be secreted, independently of the number of visits they received. In the other species—from semiarid to mesophytic habitats, with flowers with very long to medium-sized corolla tubes, visited by Diptera, Hymenoptera, or Lepidoptera—nectar production was inhibited by its removal. As a consequence, these flowers produce less nectar as a whole. This nectar saving may lead to an increase in plant reproductive success, considering that nectar sugar entails an energetic cost to the plant (Pyke, 1991). This capacity would be of particular importance for species mainly living in arid habitats.

In conclusion, results obtained so far indicate that nectar sugar composition (Galetto et al., 1998) and nectar secretion pattern (Galetto & Bernardello, 1996, this paper) seem to be conservative for the genus, i.e., these characters exhibit a low rate of change during evolution. Considering the effect of removal on nectar production, several patterns were detected. However, none of them could be clearly related to particular habitats, flower structures, or pollinator guilds of the involved *Lycium* species.

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TABLE 1.

Species and study sites for *Lycium* natural populations from Argentina. Vouchers are deposited at CORD.

Species	Locality	Voucher	Number of individual plants
L. americanum Jacq.	Córdoba: San Justo, Miramar, 11–13 Apr. 1994	*Bernardello & Galetto 758*	5
L. chilense var. *filifolium* (Miers) Bernardello	La Pampa: Toay, Parque Luro, 28–30 Nov. 1993	*Bernardello 111*	5
L. elongatum Miers	Córdoba: Capital, Barrio Cofico, 3–5 Oct. 1997	*Bernardello 879*	3
L. gilliesianum Miers	La Pampa: Toay, Parque Luro, 28–30 Nov. 1993	*Bernardello & Galetto 814*	9
L. vimineum Miers	Entre Ríos: Victoria, Isla Charigüé, 17–20 Mar. 1996	*Galetto 276*	6

TABLE 2.

Nectar concentration (C, % of sugar, mass/total mass), nectar volume (V, mL), and total milligrams of sugar (M) of five Argentine *Lycium* species.

Data on the diagonal (first measurements of each set) correspond to the nectar production pattern of each species. Flower sets were subject to different nectar removal schedules throughout the flower lifetime. Data on removal effects correspond to the mean total milligrams of sugar produced per flower. Data are mean ± sd, except for removal effect column, which are mean ± se. Measurements were taken for successive days. When nectar was not available, it was indicated with 0, whereas dashes indicate that concentration could not be measured. In the removal effect column, lowercase bold letters indicate post-hoc Bonferroni's test results and underlined data were not considered for statistical analyses because they are influenced by active resorption.

L. GILLIESIANUM

			1st Day		2nd Day		Removal Effect
Hour		**8:00**	**16:00**	**24:00**	**8:00**	**16:00**	
set 1	C	22.1 ± 4.3	66.6 ± 7.6	24.6 ± 6.1	16.5 ± 0.7	—	
	V	0.9 ± 0.4	0.2 ± 0.2	0.2 ± 0.3	0.1 ± 0.3	0	
	M	0.22 ± 0.11	0.14 ± 0.19	0.06 ± 0.08	0.02 ± 0.05	0	0.44 ± 0.05 **a**
set 2	C		69.1 ± 7.1	27.0 ± 9.5	18.0 ± 5.3	—	
	V		0.2 ± 0.1	0.9 ± 0.6	0.1 ± 0.2	0	
	M		0.20 ± 0.05	0.23 ± 0.11	0.02 ± 0.02	0	0.45 ± 0.06 **a**
set 3	C			44.6 ± 19.9	21.2 ± 4.3	—	
	V			1.8 ± 1.3	0.3 ± 0.4	0	
	M			0.67 ± 0.32	0.06 ± 0.06	0	0.73 ± 0.12 **ab**
set 4	C				48.7 ± 6.9	—	
	V				2.4 ± 1.3	0	
	M				1.43 ± 0.98	0	1.43 ± 0.4 **b**
set 5	C					75.8 ± 4.9	
	V					0.8 ± 0.4	
	M					0.8 ± 0.47	0.8 ± 0.19

L. CHILENSE VAR. *FILIFOLIUM*

		1st Day			2nd Day	Removal Effect
Hour		**10:00**	**17:00**	**24:00**	**9:00**	
set 1	C	50.0 ± 0.7	60.0 ± 0.2	37.0 ± 0.5	—	
	V	0.04 ± 0.01	0.06 ± 0.1	0.2 ± 0.5	0	
	M	0.03 ± 0.01	0.05 ± 0.07	0.08 ± 0.09	0	0.16 ± 0.08
set 2	C		52.8 ± 0.8	29.0 ± 0.4	—	
	V		0.04 ± 0.01	0.06 ± 0.1	0	
	M		0.03 ± 0.01	0.02 ± 0.04	0	0.05 ± 0.02
set 3	C			59.2 ± 0.9	—	
	V			0.1 ± 0.01	0	
	M			0.07 ± 0.01	0	0.07 ± 0.01
set 4	C				75.6 ± 4.5	
	V				0.04 ± 0.02	
	M				0.03 ± 0.02	0.03 ± 0.01

L. VIMINEUM

		1st Day			2nd Day			Removal Effect
Hour		**8:00**	**14:00**	**20:00**	**8:00**	**14:00**	**20:00**	
set 1	C	9.1 ± 1.6	24.0 ± 3.5	24.3 ± 2.8	8.7 ± 1.4	—	—	
	V	2.0 ± 0.8	1.1 ± 0.7	1.3 ± 0.7	0.9 ± 0.5	0	0	
	M	0.19 ± 0.09	0.28 ± 0.17	0.33 ± 0.17	0.09 ± 0.06	0	0	0.89 ± 0.15
set 2	C		17.3 ± 2.6	19.9 ± 2.9	5.5 ± 2.0	—	—	
	V		1.6 ± 0.6	1.0 ± 0.5	1.0 ± 0.6	0	0	
	M		0.31 ± 0.14	0.21 ± 0.09	0.05 ± 0.02	0	0	0.57 ± 0.04
set 3	C			27.0 ± 1.2	8.5 ± 1.7	—	—	
	V			1.7 ± 0.5	1.1 ± 1.2	0	0	
	M			0.52 ± 0.16	0.10 ± 0.13	0	0	0.62 ± 0.06
set 4	C				18.8 ± 1.8	7.5 ± 0.7	—	
	V				1.7 ± 0.5	1.1 ± 1.2	0	
	M				0.7 ± 0.24	0.01 ± 0.01	0	0.71 ± 0.08
set 5	C					31.9 ± 6.8	—	
	V					1.0 ± 0.6	0	
	M					0.35 ± 0.18	0	0.35 ± 0.05
set 6	C						48.9 ± 8.9	
	V						1.4 ± 0.5	
	M						0.83 ± 0.23	0.83 ± 0.08

L. ELONGATUM

		1st Day		2nd Day		3rd Day	Removal Effect
Hour		**8:30**	**18:30**	**8:30**	**18:30**	**8:30**	
set 1	C	16.4 ± 3.2	21.5 ± 0.5	—	—	—	
	V	1.9 ± 0.8	0.2 ± 0.4	0	0	0	
	M	0.31 ± 0.09	0.04 ± 0.09	0	0	0	0.35 ± 0.06 **a**
set 2	C		42.8 ± 3.4	42.0 ± 4.3	44.0 ± 1.4	30.0 ± 1.0	
	V		1.5 ± 0.5	0.6 ± 0.9	0.3 ± 0.5	0.1 ± 0.2	
	M		0.77 ± 0.27	0.31 ± 0.47	0.15 ± 0.22	0.03 ± 0.07	1.26 ± 0.34 **b**
set 3	C			43.4 ± 4.9	38.0 ± 7.8	35.0 ± 0.7	
	V			2.3 ± 0.7	0.8 ± 0.8	0.1 ± 0.2	
	M			1.16 ± 0.20	0.36 ± 0.37	0.04 ± 0.08	1.56 ± 0.22 **bc**
set 4	C				59.8 ± 11.0	—	
	V				3.4 ± 0.7	0	
	M				2.7 ± 0.96	0	2.7 ± 0.42 **c**
set 5	C					64.0 ± 6.5	
	V					2.3 ± 1.0	
	M					1.84 ± 0.67	1.84 ± 0.30

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		1st Day			2nd Day			Removal
Hour		**8:00**	**14:00**	**20:00**	**8:00**	**14:00**	**20:00**	**Effect**
set 1	C	11.6 ± 1.3	19.0 ± 7.4	9.0 ± 1.2	24.0 ± 7.0	—	—	
	V	1.9 ± 0.9	0.6 ± 0.5	0.6 ± 0.5	0.2 ± 0.2	0	0	
	M	0.22 ± 0.11	0.12 ± 0.08	0.05 ± 0.04	0.05 ± 0.07	0	0	0.44 ± 0.07 **a**
set 2	C		18.3 ± 3.4	30.5 ± 16.0	11.0 ± 4.8	—	—	
	V		2.3 ± 0.8	0.6 ± 0.6	1.4 ± 1.3	0	0	
	M		0.45 ± 0.08	0.21 ± 0.25	0.17 ± 0.19	0	0	0.83 ± 0.09 **ab**
set 3	C			17.5 ± 3.0	10.0 ± 1.2	23.7 ± 5.1	—	
	V			2.5 ± 1.1	2.0 ± 1.1	0.5 ± 0.8	0	
	M			0.45 ± 0.16	0.21 ± 0.12	0.11 ± 0.15	0	0.77 ± 0.12 **ab**
set 4	C				13.4 ± 1.9	22.4 ± 3.2	—	
	V				4.8 ± 0.8	1.0 ± 0.6	0	
	M				0.69 ± 0.22	0.22 ± 0.10	0	0.91 ± 0.1 **b**
set 5	C					26.0 ± 9.5	22.0 ± 1.4	
	V					3.3 ± 1.6	0.4 ± 0.6	
	M					0.87 ± 0.32	0.09 ± 0.12	0.96 ± 0.16 **b**
set 6	C						27.7 ± 2.9	
	V						2.0 ± 0.8	
	M						0.67 ± 0.23	0.67 ± 0.09

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THE CHROMOSOMES OF *METTERNICHIA PRINCIPIS* (SOLANACEAE) AND THEIR SIGNIFICANCE IN THE SYSTEMATIC POSITION OF THE GENUS

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ABSTRACT. The chromosomes and karyotype of *Metternichia principis* are studied for the first time. This species has $2n = 2x = 26$ and a symmetrical karyotype composed of 10 metacentric pairs, 2 meta-submetacentric pairs, and one submetacentric pair; the first pairing bears secondary constrictions related to satellites on short arms. Results are compared with previous chromosome reports in the family. The karyological data support the exclusion of *Metternichia* from the tribe Cestreae and the reestablishment of the monotypic tribe Metternichieae.

Key words: karyotype analysis, *Metternichia principis*, Solanaceae, somatic chromosome number, systematic significance.

Metternichia Mik. is a monotypic genus of Solanaceae that has been assigned to the tribe Cestreae G. Don (Hunziker, 1979; D'Arcy, 1991) and whose only species, *M. principis* Mik. ("cambará", "café-do-mato"), inhabits the Atlantic forest of Brazil, mainly in the state of Rio de Janeiro but also in Minas Gerais and Bahia. It is a tree of ornamental value, 4–6 m high, with pendent flowers 5–8 cm long, white infundibuliform corollas, fusiform and capsular fruits, very narrow winged seeds, and straight embryos (Hunziker, 1979; Freire de Carvalho, 1986; Castro Oliveira & Freire de Carvalho, 1990). As *M. principis* has never been karyologically explored, a karyotypic study was carried out with the aims of obtaining basic cytogenetic information and increasing our knowledge of its systematic relationships with other members of the family.

MATERIALS AND METHODS

All material examined came from Brazil, Estado Rio de Janeiro, Jardim Botânico do Rio de Janeiro, leg. L. Freire de Carvalho, 14 Apr. 1998. The corresponding voucher specimen, *A. Schnoor 88*, has been deposited in the herbarium of Jardim Botânico do Rio de Janeiro (RB).

Somatic chromosomes were observed in squashed root meristems obtained from seed germination and stained according to Feulgen's technique (Jong, 1997). Root tips were fixed in a 3:1 mixture of 95% ethanol:glacial acetic acid for a minimum of 12 hours at 4°C after pretreatment in a saturated solution of paradichlorobenzene in water for 2 hours at room temperature (RT). Then the root apices were stained with Schiff's reagent for 1 hour in the dark after hydrolysis in 5 N hydrochloric acid for 55 min. at RT. To make the slides permanent the coverslide was removed by freezing with CO_2 (Bowen, 1956).

Six metaphases reaching maximum chromosome contraction from four different plants were photographed with a phase-contrast Zeiss Axiophot microscope and used for chromosome measurements, which were made on prints by ruler. The chromosome classification after Levan et al. (1964), which is based in the arm ratio [r = long arm length (q) / short arm length (p)], was used with the modifications introduced by Schlarbaum and Tsuchiya (1984) as follows: *m* or metacentric (r = 1.00–1.29), *msm* or metacentric to submetacentric (r = 1.30–1.69), *sm* or submetacentric (r = 1.70–2.99). In the idiogram (Fig. 2), the chromosomes were first grouped according to their increasing arm ratio and then arranged according to the decreasing length within each group. Due to the great similarity of certain *m* chromosomes, their measurements were pooled in Table 1. The satellite length was added to the satellite-bearing arm length. Karyotype asymmetry was quantified by the intrachromosomal (A_1) and interchromosomal (A_2) asymmetry indexes (Romero Zarco, 1986), and the karyotype asymmetry categories after Stebbins (1971).

RESULTS

The somatic chromosome number $2n = 26$ was found in 56 metaphase plates from four individuals of *Metternichia principis* (Fig. 1). It is a diploid species with $x = 13$, a very rare basic chromosome number in Solanaceae. Within the family, $x = 13$ is present only in a few wild species of *Capsicum* and some cultivars of *Lycopersicon esculentum* Miller, and it is inferred to have arisen by centric (Robertsonian) fission from $x = 12$, the most frequent basic number in the family (cf. Banks, 1984; Moscone, 1989; Moscone et al., 1993).

The chromosome complement of *Metternichia principis* (Fig. 2) is composed of 10 *m* pairs (nos. 1–10), 2 *msm* pairs (nos. 11–12), and one *sm* pair (no. 13). The idiogram is based on chromosome length, the corresponding data being presented in Table 1. The average chromosome length is 1.50 µm and the total length of the haploid complement reaches 19.50 µm. Due to the lack of chromosomal markers by the applied Feulgen's classical staining procedure, it was not possible to distinguish among the 10 *m* chro-

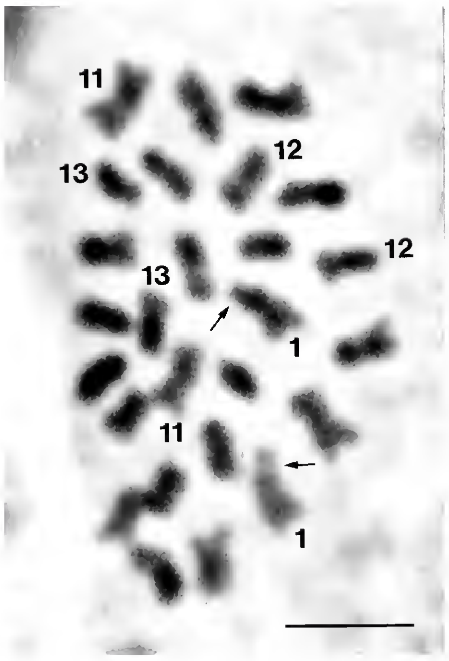

Figure 1. Mitotic metaphase of *Metternichia principis* (2*n* = 26). The identified homologous chromosomes are pointed out. Arrows indicate secondary constrictions related to satellites. Scale bar = 3 µm.

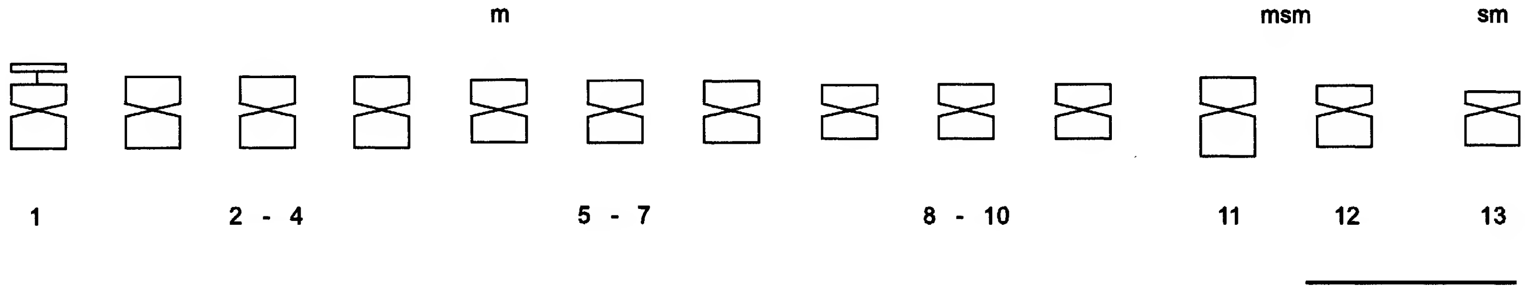

Figure 2. Idiogram of *Metternichia principis* (2*n* = 26). Scale bar = 5 µm.

TABLE 1.

Measurements of somatic chromosomes of *Metternichia principis*. Abbreviations: *r* = arm ratio; q = long arm length; p = short arm length; c = chromosome length; HKL = haploid karyotype length; sat = satellite; x = mean value; sd = standard deviation.

Pair No.	Chromosome Lengths (µm): x (sd)			Relative Length (% of HKL)	*r* (q/p) x (sd)	Chromosome Type
	p	q	c			
1	0.81 (0.12)	0.92 (0.09)	1.73 (0.20)	8.87	1.14 (0.10)	m (sat)
2–4	0.77 (0.05)	0.92 (0.07)	1.69 (0.11)	8.67	1.20 (0.09)	m
5–7	0.69 (0.06)	0.78 (0.04)	1.47 (0.09)	7.54	1.13 (0.06)	m
8–10	0.57 (0.05)	0.68 (0.06)	1.25 (0.12)	6.41	1.19 (0.02)	m
11	0.75 (0.06)	1.11 (0.08)	1.86 (0.08)	9.54	1.48 (0.18)	msm
12	0.56 (0.02)	0.86 (0.09)	1.42 (0.11)	7.28	1.53 (0.14)	msm
13	0.42 (0.04)	0.84 (0.06)	1.26 (0.10)	6.46	2.00 (0.11)	sm

mosomes with certainty except pair no. 1, which bears secondary constrictions related to satellites of variable size on the short arms. The remaining 9 *m* chromosome pairs were subdivided in three groups according to their decreasing size (pairs nos. 2–4, 5–7, and 8–10); within each group the individual lengths were pooled into average values.

The karyotype of *Metternichia principis* is symmetrical, with $A_1 = 0.201$ and $A_2 = 0.142$, belonging to the 1A category of Stebbins's (1971) classification. Within the family Solanaceae, symmetrical karyotypes with a majority of *m* chromosomes as exhibited by *M. principis* are common to many genera with $x = 12$ (Moscone, 1989). In many angiosperms, karyotypes with high symmetry are correlated with the primitive or plesiomorphic condition of the taxa, whereas asymmetrical ones indicate a derived or apomorphic stage (Stebbins, 1971). Nevertheless, despite its symmetric karyotype, the presence of $x = 13$ and other specialized macromorphological characters like very narrow and winged seeds with scanty endosperm and zygomorphic calyx with unequal sepals in *M. principis* suggest an evolutionarily derived position.

DISCUSSION

The arm ratio-based chromosome classification proposed by Schlarbaum and Tsuchiya (1984) was found to be more useful than the one suggested by Levan et al. (1964) because it discriminated an additional morphological category of chromosomes with high symmetry (*msm*). According to Levan et al.'s (1964) system the haploid karyotype formula of *M. principis* is 12 *m* + 1 *sm*, but after Schlarbaum and Tsuchiya's (1984) terminology is 10 *m* + 2 *msm* + 1 *sm*. In this particular taxon, chromosome identification by the classical staining methods such as the one employed herein is limited by the small chromosome size and karyotype uniformity. Therefore, the application of chromosome banding techniques to reveal heterochromatic regions potentially useful as genetic markers is warranted.

In the tribe Cestreae, where *Metternichia* has been placed (Hunziker, 1979; D'Arcy, 1991), karyological information for other genera indicates that *Cestrum* L. and *Vestia* Willd. have $x = 8$ (cf. Schnack & Covas, 1947; Goodspeed, 1954; Tschischow, 1956; Roe, 1967; Sobti et al., 1979; Moscone, 1992), while *Sessea* Ruiz & Pav. remains unknown. Although there are no data concerning chromosome size in *Vestia*, the species of *Cestrum*, with an average chromosome length of 10–12 µm (Berg & Greilhuber, 1993; Moscone, unpublished), exhibit the largest chromosomes in the family. In contrast, *M. principis* reveals the smallest chromosomes known thus far, together with the species of *Solanum* sect. *Basarthrum* (Bitter) Bitter (cf. Bernardello & Anderson, 1990); the latter genus belongs to the tribe Solaneae Miers and is characterized by comparatively small chromosomes except for the members of section *Cyphomandropsis* Bitter (Moscone, 1992).

Our particular chromosome findings—the unusual chromosome number and size—together with several macromorphological and palynological features, such as (1) the very narrow and large (30–39 mm long) winged seeds with scanty endosperm, (2) cotyledons equally as wide as the rest of the embryo, (3) hilum not far from the proximal end of the radicle, (4) zygomorphic calyx with unequal sepals, (5) contorted-conduplicate corolla aestivation, (6) cyathium absent, (7) exserted anthers, and (8) pollen with echinate exine, determine that *Metternichia* is distinct from the other members of Cestreae and, at the same time, it constitutes a unique taxon within the family. One should remember that Solanaceae display the following typical morphological states: seeds usually small, if large up to 8 mm long, and with different forms but never javelin-shaped as in *Metternichia*; embryo with rather abundant endosperm and cotyledons as wide as the rest of the embryo; actinomorphic calyx with equal lobes or entire margin; variable corolla aestivation although contorted-conduplicate in Datureae G. Don; cyathium exceptional; and pollen with variable exine ornamentation but rarely exine echinate. On the other hand, Cestreae are particularly characterized by subpolyhedric or compressed seeds not exceeding 8 mm in length and with abundant endosperm, winged only in *Sessea*; cotyledons broader than the rest of the embryo and hilum away from the radicle; actinomorphic calyx with equal lobes; valvate-induplicate or slightly contorted corolla aestivation; cyathium present; generally included anthers; and pollen with striate or rugulate exine (Hunziker, 2001).

It should be noted that the isolated position of *Metternichia* in the family is also supported by chloroplast *rbc*L gene sequence data (Fay et al., 1998). Thus, the exclusion of this genus from Cestreae and the reestablishment of the monotypic tribe Metternichieae Miers are suggested (Hunziker, 2001).

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This paper is dedicated to the memory of Dr. William G. D'Arcy, who has been a mentor in Solanaceae systematics. We thank Dr. G. Barboza for comments on the manuscript and Mr. R. Münch for helping with the software to design the idiogram. Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, and Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba (Argentina), are acknowledged for economic support.

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MORPHOLOGY OF FOLIAR TRICHOMES IN SPECIES OF *SESSEA* (SOLANACEAE)

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Abstract. A morphological study of the different types of foliar trichomes in 19 *Sessea* species was made in order to assess their value as taxonomic criteria for species delimitation. Characteristics such as form, density, indumentum, and trichome distribution on the leaf surface were examined. An extraordinary diversity was revealed among these features. In this work four basic trichomatic types are described, each one with several subtypes. The dendritic hair type was exhibited by almost all the studied species.

Key words: *Sessea*, Solanaceae, trichome morphology.

Sessea Ruiz & Pav. is one of the genera belonging to the tribe Cestreae. Members of this genus are characterized as follows: unarmed trees with pubescence of simple or branched hairs. Leaves simple, entire, pinnately nerved, mostly glabrate above; mostly short-petiolate; minor leaves sometimes present. Inflorescences axillary and pseudoterminal, few- or many-flowered racemes, spikes or cymes, often large and appearing paniculate; bracts often present. Flowers mostly 5-merous, pedicellate, bracteolate; calyx small, cupular or tubular, mostly shallowly lobed; corolla narrowly tubular, much exceeding the calyx, lobed, the lobes narrow, shorter than the tube, spreading or reflexed when open. Stamens inserted in the corolla tube at similar levels, the insertion levels varying greatly in different species, the adnate portion mostly evident from the corolla base, the insertion variously pubescent or tumid, anthers small, located together at the corolla mouth. Ovary generally shorter than the calyx, 2-locular, ovules 4 to 16, style slender, stigma capitate or variously lobed, small, in at least some species oblique at the style apex. Fruit a narrowly ellipsoid or ovoid, terminally dehiscent capsule; seeds varying in number, ovoid, surrounded by a hyaline wing; embryo straight (Benítez de Rojas & D'Arcy, 1998).

The value of trichome morphology as a taxonomic criterion in plants is well known. Some families can be easily identified by the presence of a type or several types of hairs; in other cases the hairs are of great significance for separating genera and species (Metcalfe & Chalk, 1950; Metcalfe, 1963; Carlquist, 1961). Trichomes have been of considerable help in the taxonomy of Solanaceae, especially in the understanding of the different taxa in the tribe Anthocercidae (Haegi, 1991), in the genus *Nicotiana* (Goodspeed, 1964), *Solanum* sect. *Basarthrum* (Seithe & Anderson, 1982), *Solanum* sects. *Cernuum* and *Lepidotum* (Carvalho & Machado, 1991), *Physalis* (Seithe & Sullivan, 1990), and also in other *Solanum* sections.

The genus *Sessea* was first revised by Bitter (1922), who segregated 13 species into four series using trichome morphology, among other characteristics. It was revised again by Francey (1934), who ignored the series of Bitter and recognized 23 species. Most of these taxa show a dense tomentum of branched hairs, which has been used as a criterion to distinguish them.

Seithe (1962, 1979) used the form of the trichomes as a criterion for distinguishing the numerous taxa of *Solanum*. On the basis that trichomes in *Sessea* are considered to be a relevant diagnostic characteristic, in this work 19 species of *Sessea*, including four species that Bitter (1922) did not consider because they were published after his conspectus, are examined and grouped considering and assessing trichome types as a taxonomic criterion.

MATERIALS AND METHODS

Trichomes from leaves were obtained from herbarium material of species of *Sessea* (Table 1). Fragments of leaves were boiled in water for 30 minutes, and then placed in sodium hypochlorite (5.25%) for variable periods at room temperature until both surfaces of the epidermis were separated. Then they were washed with distilled water and stained with an aqueous toluidine blue solution (0.5%). Semi-permanent mountings in water:glycerin (1:1) were made for microscopic examination. Trichomes were also obtained by scraping the surface of the leaves from herbarium material with a razor blade. Mountings were made as above. Photographic documentation of foliar trichomes was obtained with a digital Canon Power Shot S40 camera. The following procedures were considered when describing the trichomes: examination of the overall surface appearance (indumentum), morphology of individual trichomes, and trichome complement. The terminology used was that of Seithe (1979).

The density was not quantified, and because the trichomes were scarce or absent on the adaxial surface of most species, their characterization was made only on the abaxial surface using an optic microscope.

RESULTS

There are four clearly recognizable trichomes, each one with several subtypes found mainly on the abaxial leaf surface among species of *Sessea*. These are mentioned as trichome types as follows:

Type 1. Eglandular, simple, uniseriate unbranched hairs.

- Subtype A: Papillae (Fig. 1B, 1C)
- Subtype B: Short or long unicellular (Fig. 1A)
- Subtype C: Multicellular (Fig. 1D, 1E)
- Subtype D: Multicellular with projections (Fig. 1F)

Type 2. Eglandular branched hairs: multicellular, dendroid with branches having an emergent cell at several levels and planes.

- Subtype A: Bifurcate (Fig. 2H)
- Subtype B: Narrow branches with acute extremes (Fig. 2A, 2B, 2D, 2E, 2F, 2G, 2J, 2K)
- Subtype C: Wide, short branches with obtuse extremes (Fig. 2I)
- Subtype D: Delicate branches with fine walls (Fig. 2C)

Type 3. Glandular, simple, uniseriate hairs.

- Subtype A: Stalk uni- or bicellular and head unicellular (Fig. 3B, 3C, 3D, 3H, 3I)
- Subtype B: Stalk uni- or bicellular and head bicellular (Fig. 3A, 3E, 3J)
- Subtype C: Stalk bicellular and head tetracellular (Fig. 3F)
- Subtype D: Stalk with more than two cells and head uni- or bicellular (Fig. 3K)
- Subtype E: Stalk with more than two cells with projections of different sizes and head unicellular (3G)

Type 4. Mixed, short or long hairs with acute or obtuse extremes and some of its branches ending in a unicellular head.

- Subtype A: Short hair
- Subtype B: Long hair (Fig. 4)

Table 2 summarizes the types and subtypes of hairs observed in each species on the abaxial surface. Few trichomes were found on both surfaces of *Sessea colombiana*, *S. corymbiflora*, and *S. confertiflora*, species that appear to be glabrous to the naked eye. In the first and second species, glandular stalked trichomes with unicellular and bicellular heads were observed (Subtypes 3A, 3B), while in *S. confertiflora* eglandular bicellular uniseriate trichomes were observed (Subtype 1C), along with glandular trichomes with uni- or bicellular stalked and unicellular heads (Fig. 3B) (Subtype 3A).

The species *Sessea brasiliensis*, *S. dependens*, *S. discolor*, *S. elliptica*, *S. farinosa*, *S. hypotephrodes*, *S. lehmanni*, *S. macrophylla*, *S. regnellii*, and *S. tipocochensis* have trichomes on both surfaces.

The eglandular unicellular or multicellular uniseriate trichomes (Type 1) are infrequent in the studied species. The Subtype B was observed in *Sessea brasiliensis*, *S. dependens* (Fig. 1A), *S. farinosa*, and *S. hypotephrodes*, while the multicellular uniseriate trichomes (Subtype C) were found in *S. confertiflora*, *S. lehmanni* (Fig. 1D), *S. macrophylla* (Fig. 1E), and *S. regnellii* (Fig. 1F).

The eglandular branched hairs (Type 2) were located primarily on the abaxial surface, being the only type of hair in four of the 19 studied species where they are present in high densities: *Sessea acuminata* (Fig. 2A), *S. andina* (Fig. 2B), *S. crassivenosa,* and *S. vestita* (Fig. 2J, 2K). They also are abundant in *S. discolor* (Fig. 2D) and *S. sodiroi*. In these species, glandular trichomes (Subtype 2A) are present on the adaxial surface. In *S. stipulata*, even when the dendritic trichome was also the only type of hair observed, its density was intermediate in relation to the aforementioned species and the rest of the taxa in which they were in low densities and mixed with other types of trichomes. The branched trichomes found in *S. brasiliensis* and in either high or low densities in *S. dependens* are made up of cells with very fine walls that collapse forming amorphous masses over the surfaces (Fig. 2C). In the case of *S. lehmanni*, the branches of the trichomes are shorter than in the rest of the species (Fig. 2F). A variant of the typical dendritic hair was observed in *S. tipocochensis* (Fig. 2I); its cells were

TABLE 1.

Material examined.

Taxon	Location	Collector and Number	Herbarium
S. acuminata Francey	Colombia: Quindio. Mpio. de Salento. Vereda Cocora	*W. Vargas 643*	MO
S. andina Francey	Ecuador: Morona-Santiago	*H. van der Werff & E. Gudiño 11095*	MO
S. brasiliensis Toledo	Brazil: São Paulo	*F. C. Hoehne 184*	SP
S. colombiana Francey	Venezuela: Trujillo-Boconó	*C. E. Benítez et al. 5634*	MY
S. confertiflora Francey	Peru: Lima-Canta	*A. Granda Paucar 1100*	MY
S. corymbiflora Goudot ex Rich. Taylor & R. Phillips	Venezuela: Táchira-Pregonero	*C. E. Benítez et al. 4741*	MY
S. crassivenosa Bitter	Ecuador: Chimborazo-Cañar 6	*W. H. Camp 4069*	US
S. dependens Ruiz & Pav.	Bolivia: Cochabamba-Chapare	*J. Steinbach 9814*	MO
S. discolor Francey	Peru: Cusco-Calca	*C. Vargas 3604*	CUZ
S. elliptica Francey	Colombia: Boyacá-Cañutal	*J. Cuatrecasas 1790*	US
S. farinosa (Urb. & Ekman) Francey	Haiti: La Selle	*E. L. Ekman 7884*	US
S. hypotephrodes Bitter	Bolivia: Sta Cruz-Amboro	*R. Jardim & A. Abbott 2100*	MO
S. lehmanni Bitter	Colombia: Valle del Cauca-Bugalagrande	*W. Devia & F. Prado 1946*	MO
S. macrophylla Francey	Venezuela: Táchira-San Vicente de la Revancha	*C. E. Benítez et al. 5649*	MY
S. regnellii Taub.	Brazil: Paraná-Mandirituba	*G. Hatschbach & J. M. Silva 51480*	MO
S. sodiroi Bitter	Ecuador: Chimborazo-Pallatanga	*J. L. Clark et al. 1388*	QCNE
S. stipulata Ruiz & Pav.	Peru: Huánuco-Huarmiragua	*A. Granda Paucar 1745*	MY
S. tipocochensis (Werderm.) Francey	Ecuador: Cañar-Moloboc	*W. Zak 2445*	MO
S. vestita (Hook. f.) Miers	Ecuador: Imbabura-Veracruz	*W. Zak 3429*	MEXU
S. vestita (Hook. f.) Miers	Ecuador: Pichincha-Pululahua	*L. Holm-Nielsen et al. 5174*	AAU

TABLE 2.

Indumentum and hair types and subtypes in *Sessea* species.

Species	Indumentum	Type 1: Eglandular unbranched hairs				Type 2: Eglandular branched hairs				Type 3: Glandular hairs					Type 4: Mixed hairs	
		A	B	C	D	A	B	C	D	A	B	C	D	E	A	B
S. acuminata	Pannose						X									
S. andina	Pannose						X									
S. brasiliensis	Glabrate		X						X	X	X					
S. colombiana	Glabrate									X	X					
S. confertiflora	Glabrate			X						X						
S. corymbiflora	Glabrate									X	X					
S. crassivenosa	Tomentulose						X									
S. dependens	Farinaceous		X						X	X	X					
S. discolor	Tomentulose						X			X		X				
S. elliptica	Pannose						X			X						
S. farinosa	Farinaceous	X	X				X			X					X	
S. hypotephrodes	Tomentose		X				X			X						
S. lehmanni	Farinaceous			X			X			X		X				
S. macrophylla	Tomentose			X			X			X	X	X			X	
S. regnellii	Tomentose			X	X	X	X			X				X	X	
S. sodiroi	Tomentulose						X			X						
S. stipulata	Pannose						X			X						
S. tipocochensis	Villous							X	X	X			X			X
S. vestita	Pannose						X									

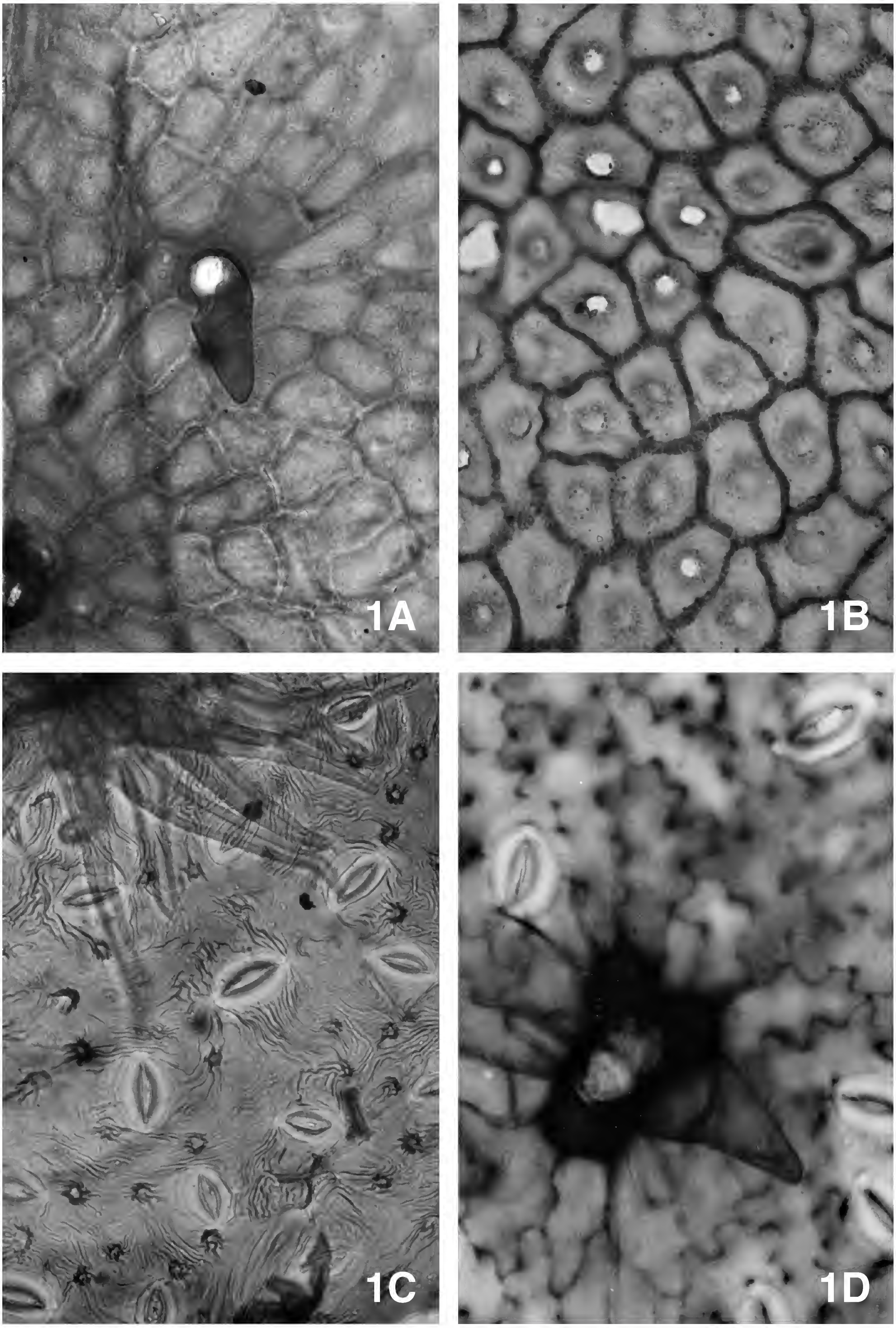
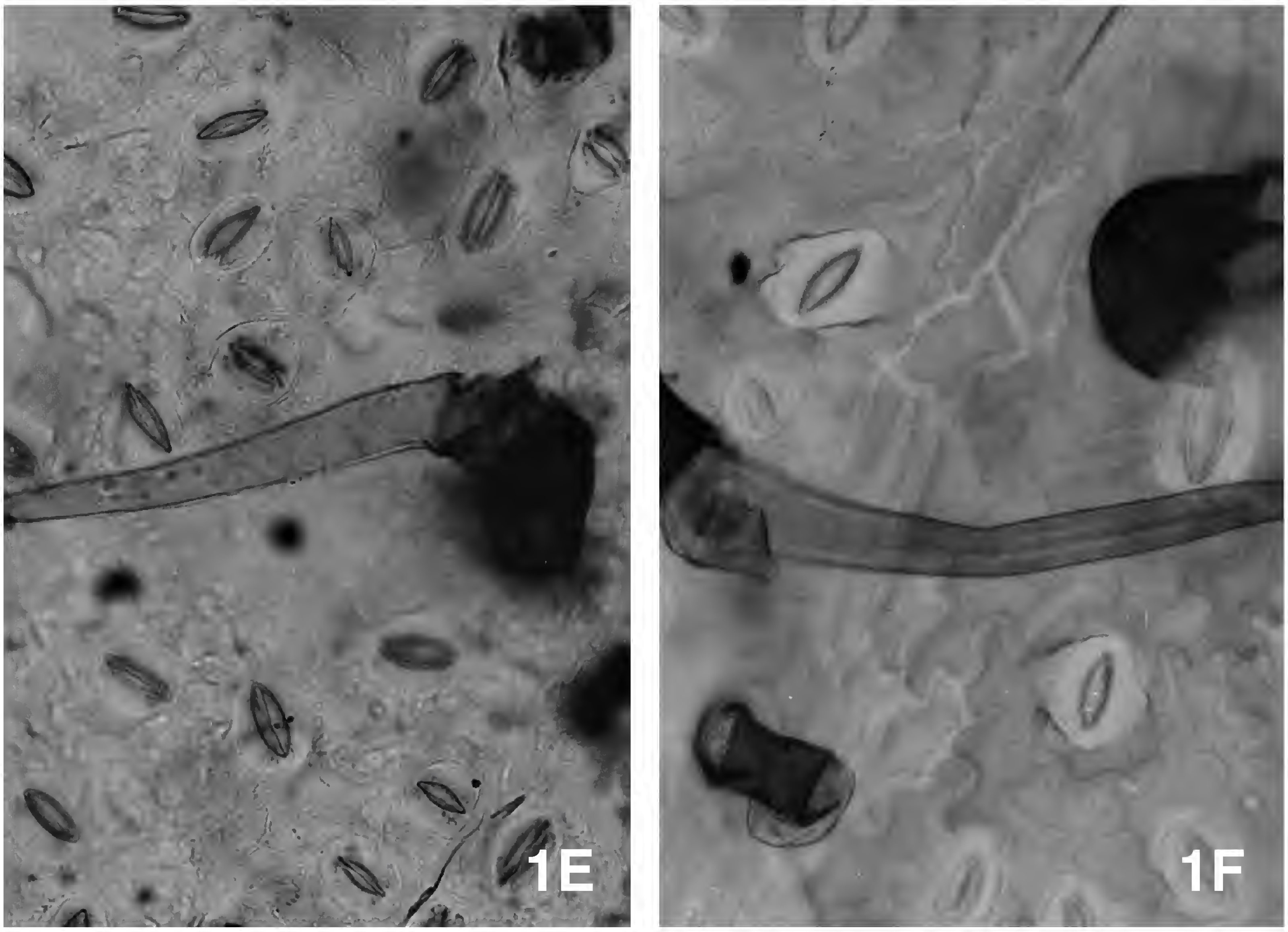


Figure 1. Eglandular trichomes in *Sessea*. —A. *S. dependens*. —B, C. *S. farinosa*. —D. *S. lehmanni*. —E. *S. macrophylla*. —F. *S. regnellii*. Magnification × 400.



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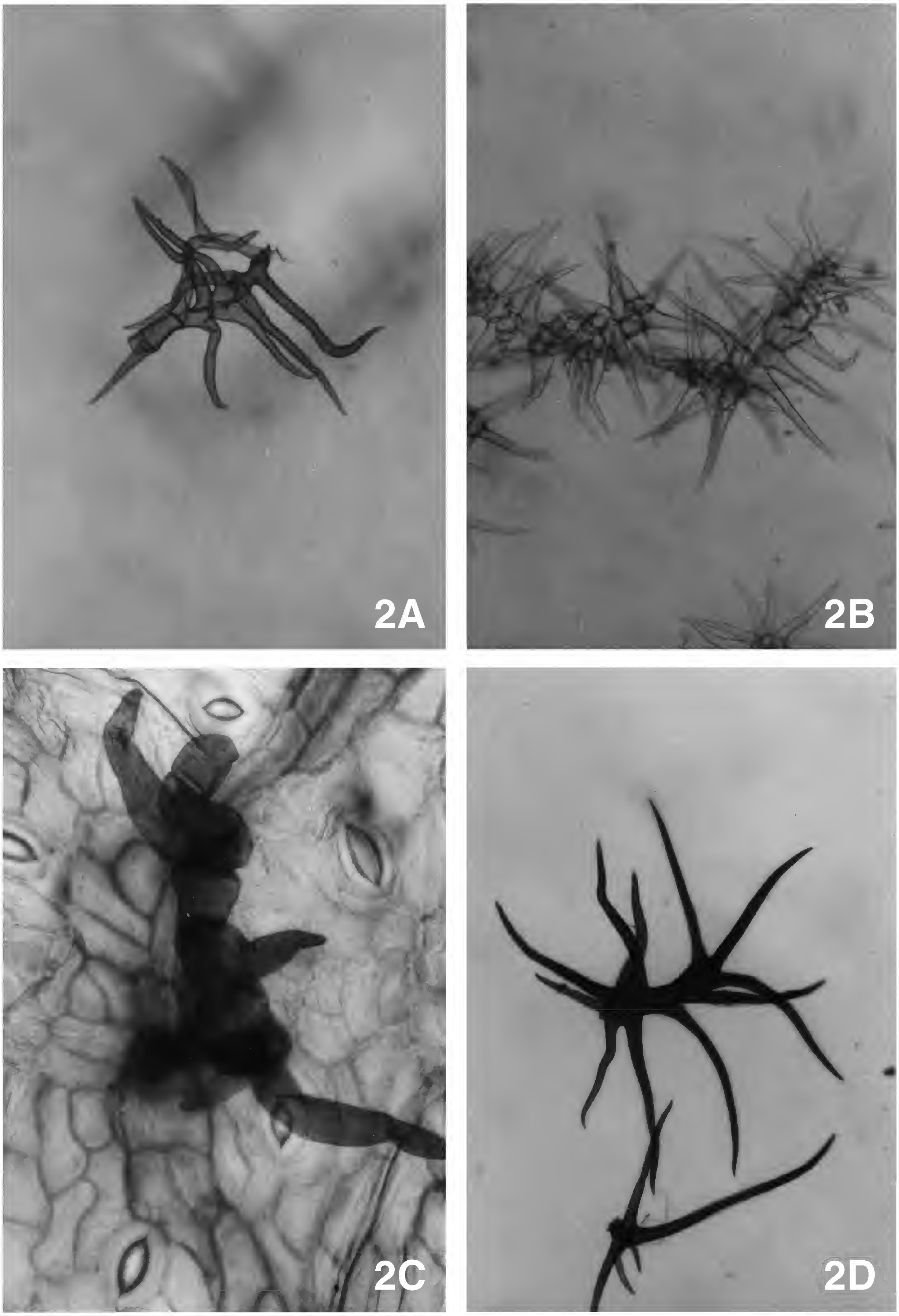
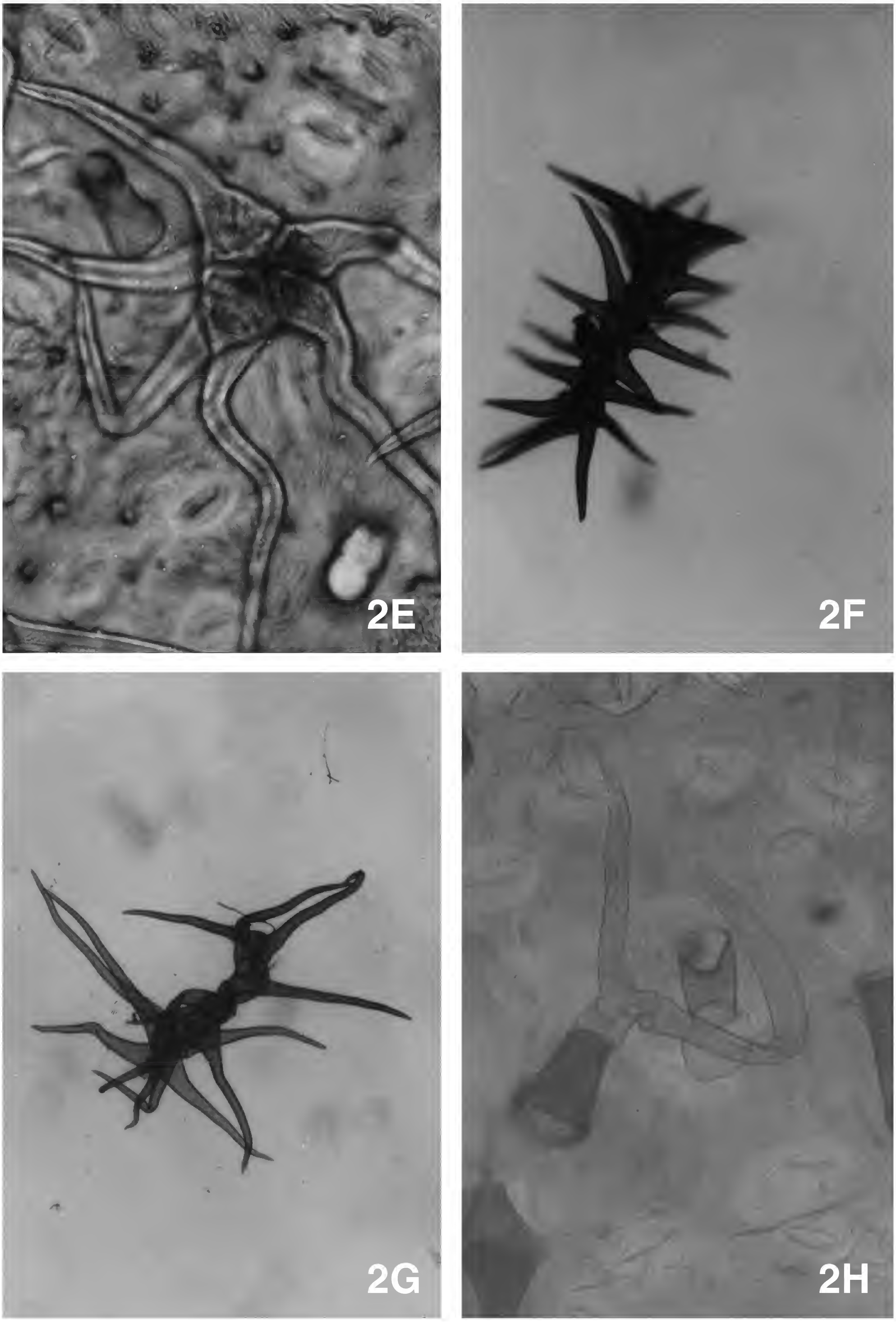


Figure 2. Branched trichomes in *Sessea.* —A. *S. acuminata*. —B. *S. andina.* —C. S. *brasiliensis.* —D. *S. discolor.* —E. *S. farinosa.* —F. *S. lehmanni.* —G. *S. hypotephrodes.* —H. *S. regnellii.* —I. *S. tipocochensis.* —J, K. *S. vestita*. A, B, D, F, G, J, magnification × 100; C, E, H, I, K, × 400.



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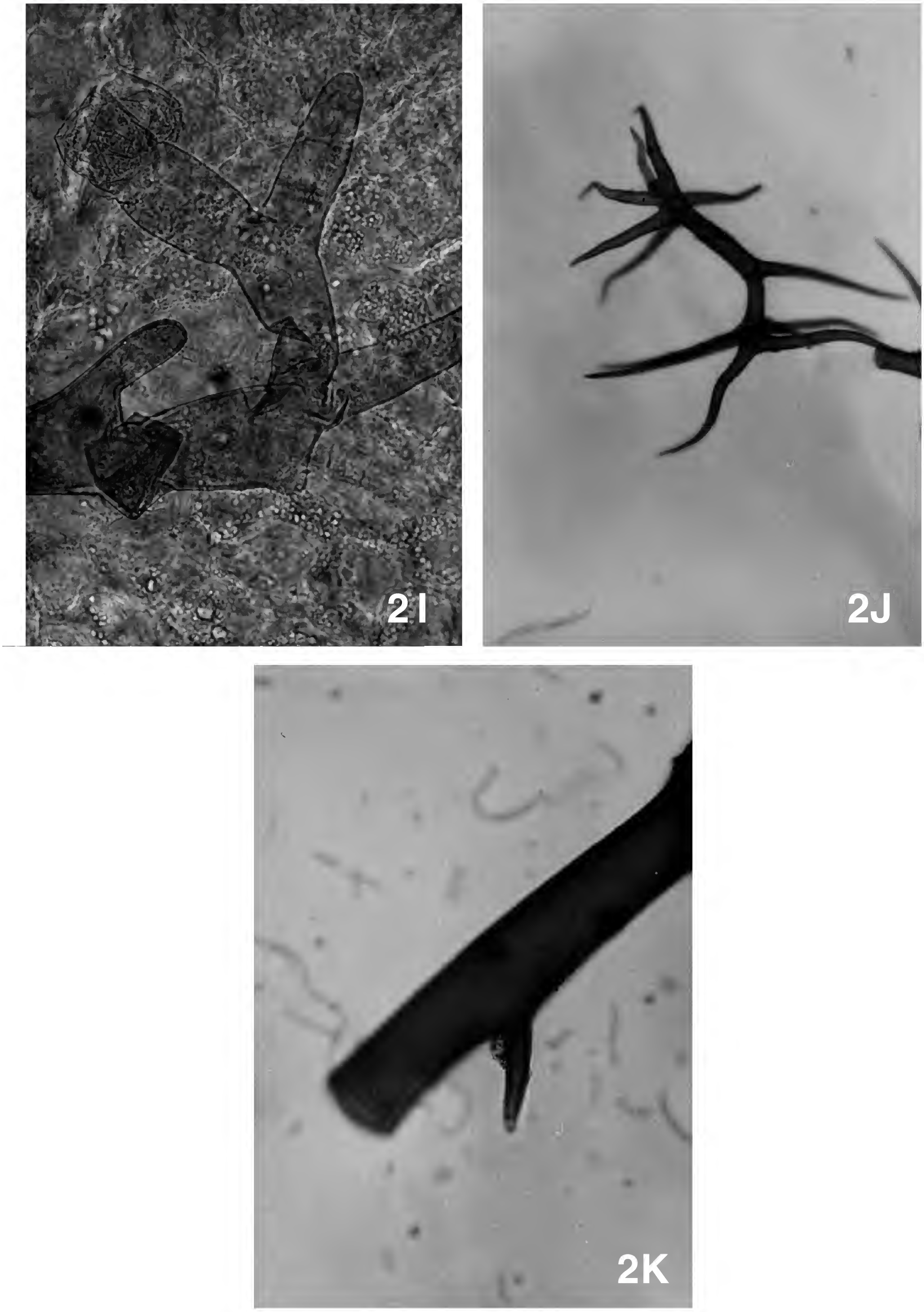

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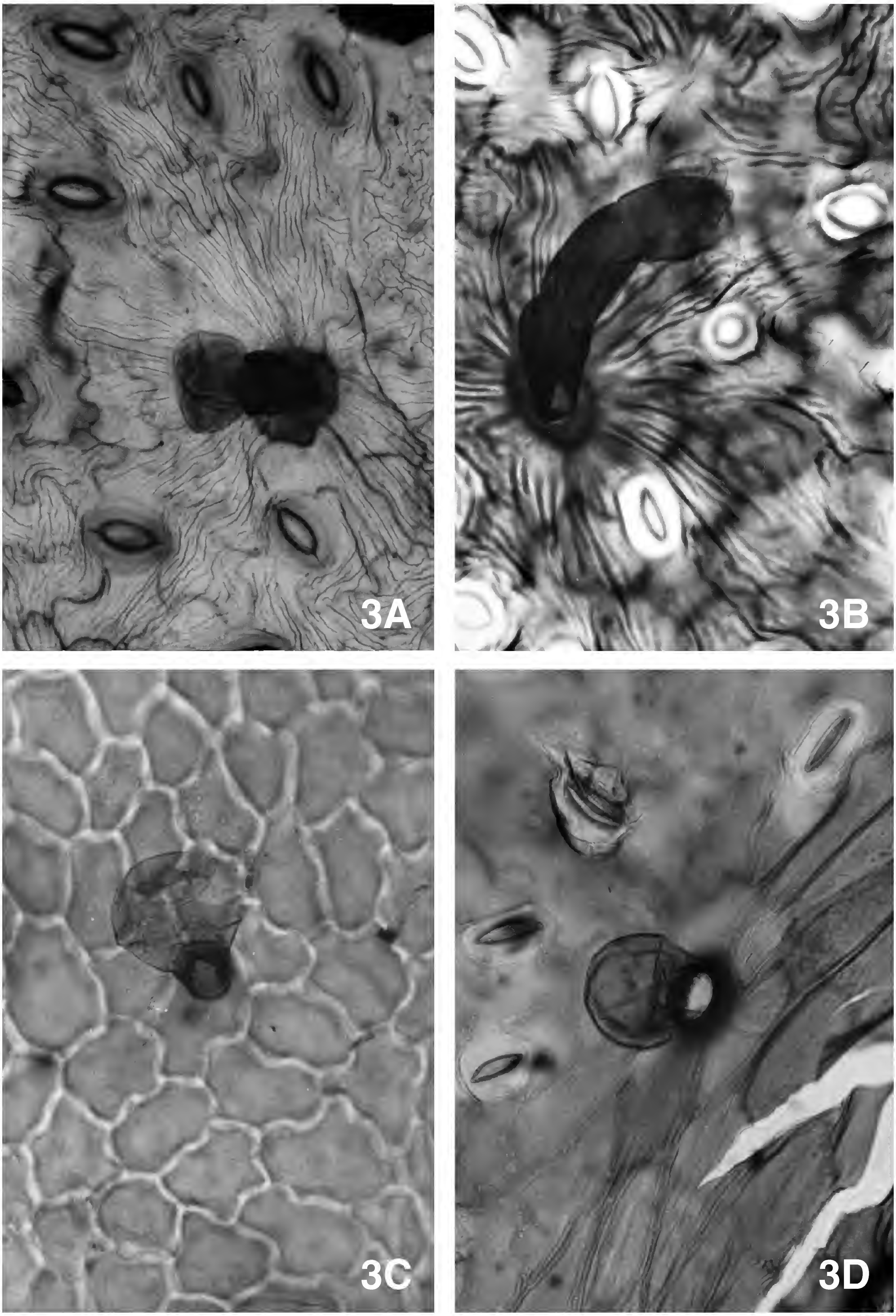
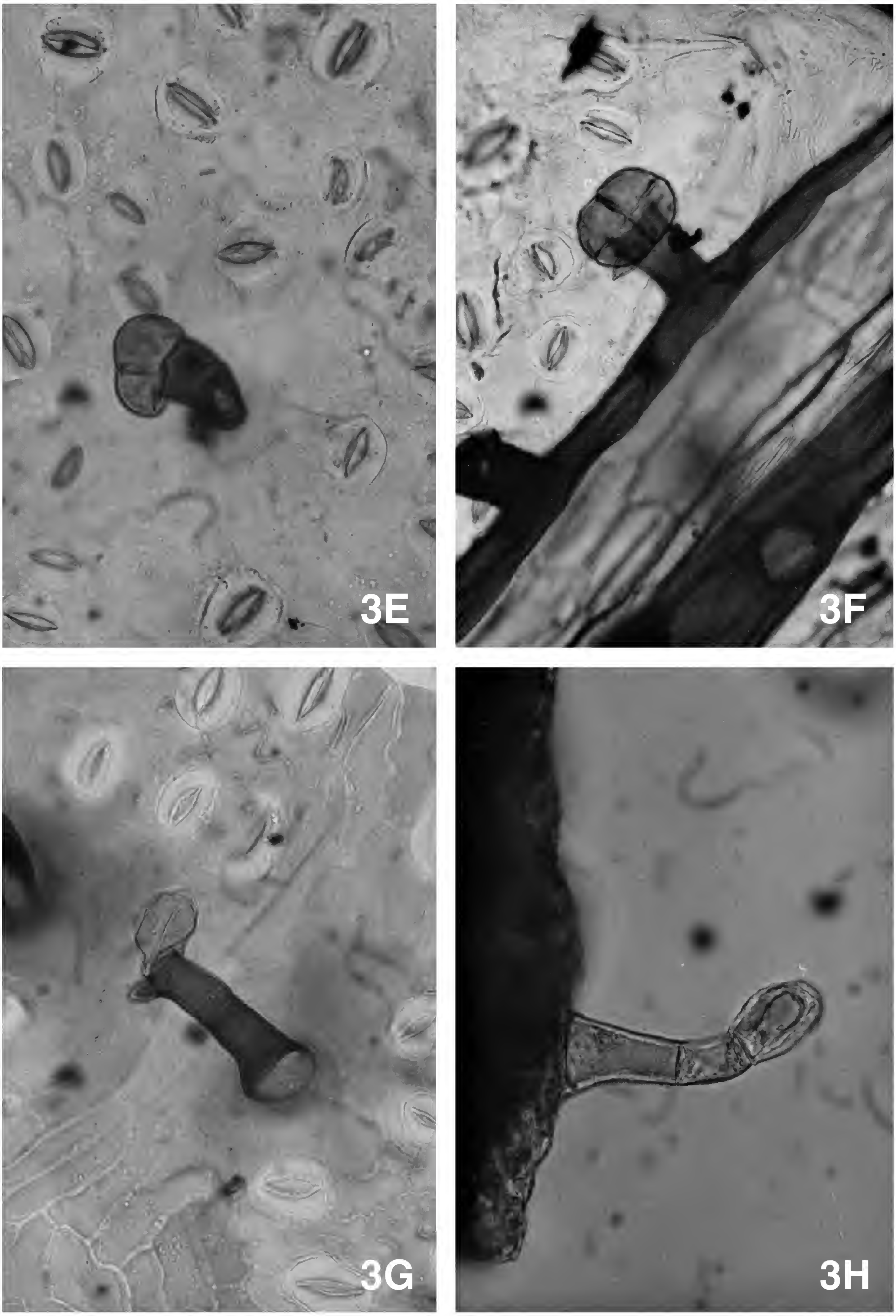


Figure 3. Glandular trichomes in *Sessea*. —A. *S. brasiliensis*. —B. *S. confertiflora*. —C. *S. elliptica*. —D. *S. lehmanni*. —E, F. *S. macrophylla*. —G, H, I. *S. regnellii*. —J, K. *S. tipocochensis*. Magnification × 400.



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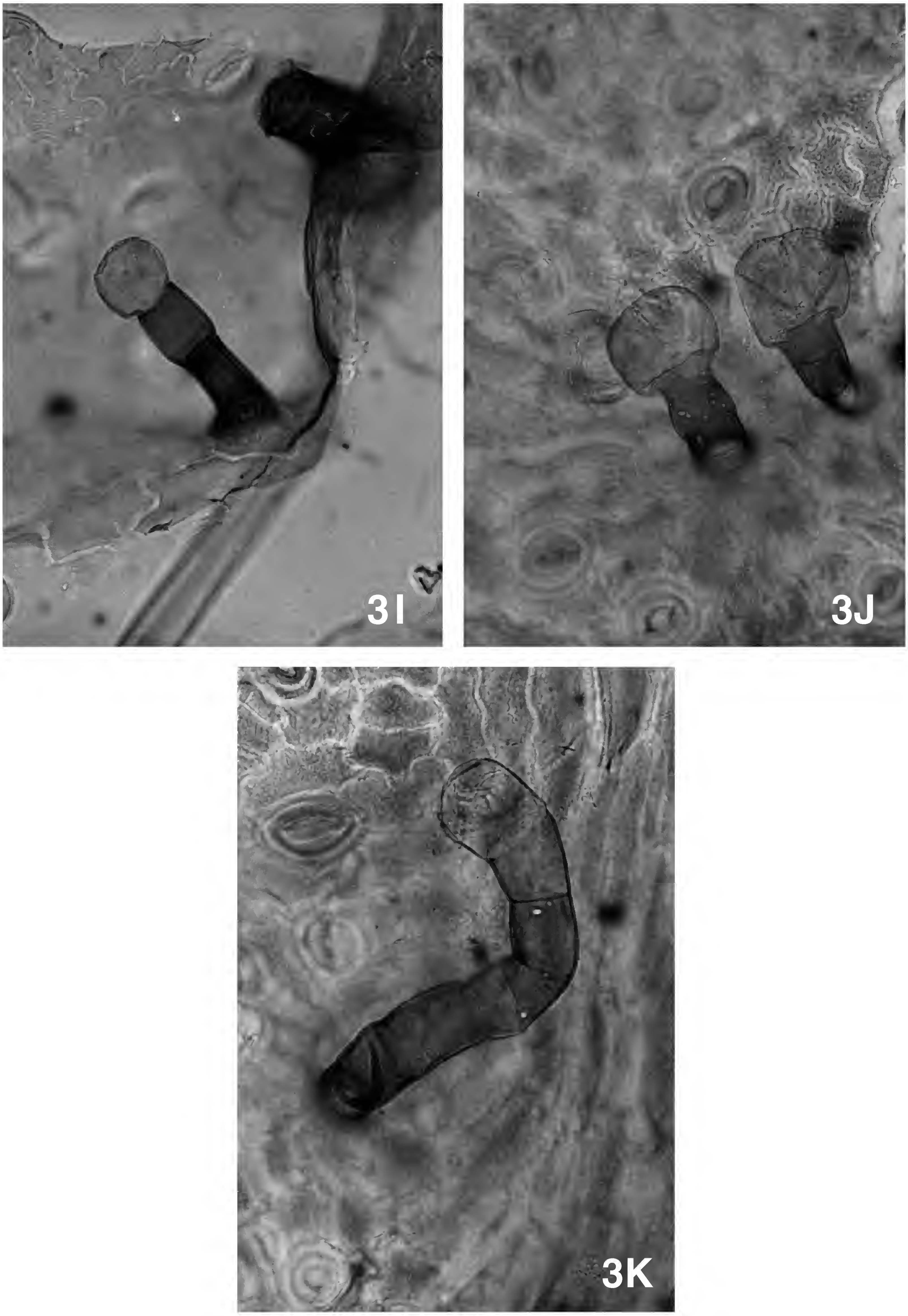

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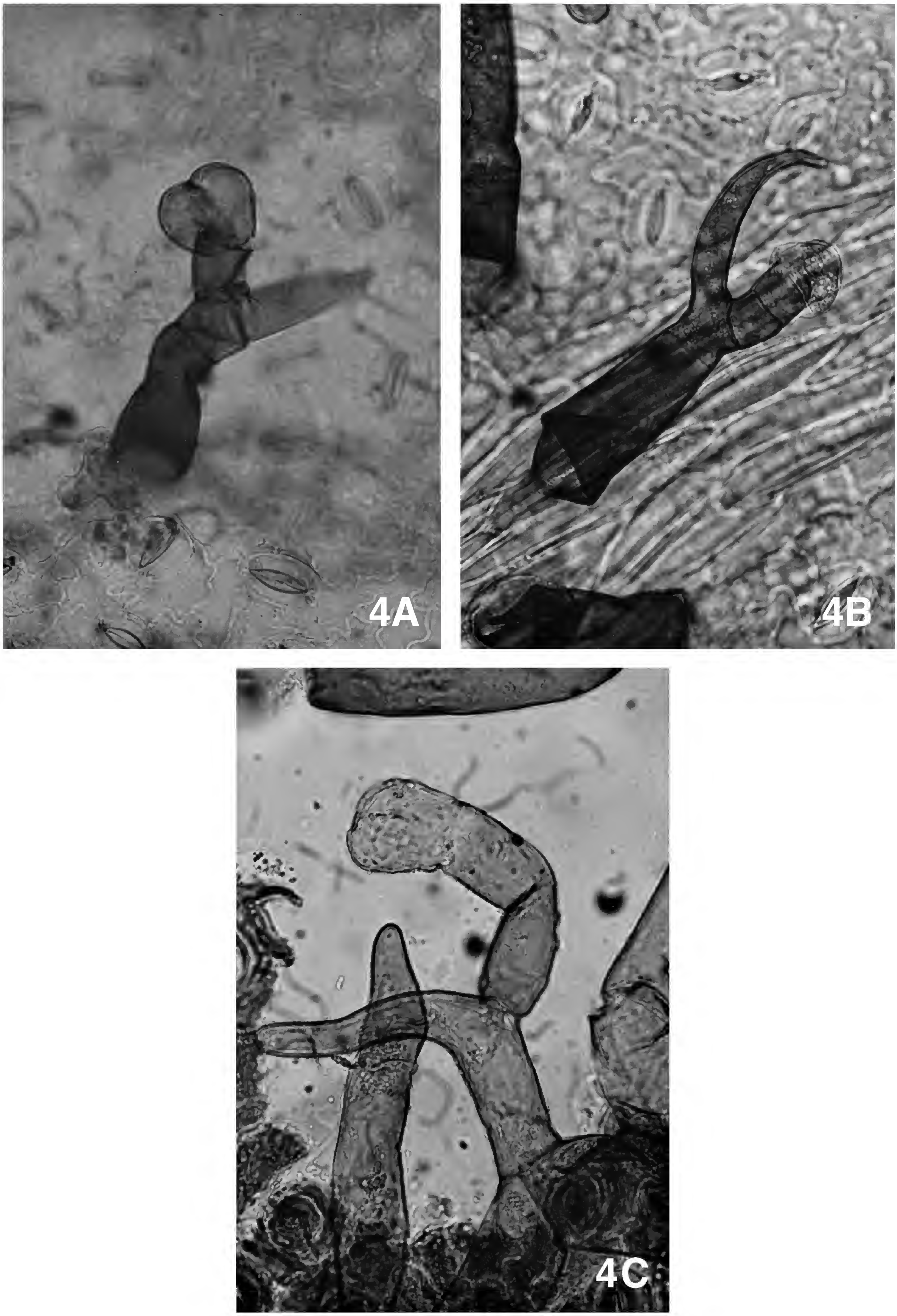

Figure 4. Mixed trichomes in *Sessea*. —A. *S. macrophylla*. —B. *S. regnellii*. —C. *S. tipocochensis*. Magnification × 400.

ribbon-like and wider with obtuse extremities. In *S .vestita* the branched trichomes bear little projections (Fig. 2J, 2K). In *S. regnellii* the trichomes are bifurcate (Fig. 2H).

The Subtype A of glandular trichomes is made up of one to two cells at the foot and one cell at the head (Fig. 3B, 3C, 3D, 3H, 3I). This type was observed in all the species that have trichomes on both surfaces. The species *S. discolor*, *S. lehmanni*, and *S. macrophylla* (Fig. 3F) have glandular trichomes with tetracellular heads, in addition to Subtype A. In *S. regnellii* there is a particular variant where foot cells may possess projections (Fig. 3G). In the case of *S. tipocochensis*, the glandular trichomes are straight, bent, longer, and with relatively wider cells (Fig. 3K).

The species with mixed trichomes are *Sessea farinosa*, *S. macrophylla* (Fig. 4A), *S. regnellii* (Fig. 4B), and *S. tipocochensis* (Fig. 4C), the first two bearing similar types with short, acute tip branches. In *S. tipocochensis* the branch tips are longer and obtuse.

DISCUSSION

The diversity of trichomes in species of Solanaceae has been demonstrated and applied as a taxonomic criterion for delimitation at the specific level (Seithe, 1979; Subils, 1989; Ogundipe, 1992).

Bitter (1922), in a conspectus of *Sessea* on the basis of morphology of reproductive and vegetative features, drew attention to the presence of the candelabra-like (= dendritic) hairs. In this manner he arranged the following species with high density of that kind of trichomes, among other characters, in the Series I *Pilosivertex* Bitter: *S. crassivenosa*, *S. elliptica*, *S. hypotephrodes*, *S. stipulata*, *S. sodiroi*, *S. discolor*, and *S. vestita*. The hair density, although not quantified, varies among the cited species and enables taxonomic consideration of indumentum types: pannose, tomentose, or tomentulose (Table 2).

In the Series II *Psilandra* Bitter with very short hairs in the vegetative parts, Bitter included *Sessea lehmanni*. The dendritic trichomes of this species show very short branches in relation to the rest of the species.

At the same time, the species *Sessea dependens* and *S. brasiliensis* have short, delicate, and dendritic hairs. The first one was placed in the Series III *Pendulisessea* Bitter, where the trichomes were characterized as candelabra-like, short and partially pseudostellate, while the second species, which was described after the conspectus of Bitter, was not considered by him.

With respect to *Sessea regnellii*, placed in the Series IV *Proseoa* Bitter and described as having candelabra-like trichomes, seven subtypes of hairs were found. Some of these are restricted to this species, for instance, trichome Subtypes 2A and 3E. The species *S. colombiana*, *S. confertiflora*, and *S. corymbiflora* do not have dendritic hairs in correspondence with the Series V *Calvivertex* Bitter.

The species *Sessea andina*, *S. brasiliensis*, *S. farinosa*, *S. macrophylla*, and *S. tipocochensis* were not considered by Bitter because they were described after his conspectus. These show the following features: *S. andina* has a high density of dendritic trichomes on the abaxial epidermis, a similar trait to species placed by Bitter in Series I. *Sessea farinosa* has papillae and mixed trichomes. Perhaps the existence of papillae confers to this species the feature of farinaceous leaves as described by Urban and Ekman (1929). *Sessea macrophylla* and *S. tipocochensis* exhibit mixed trichomes, but in *S. tipocochensis* these are more abundant and long, and the branches are wide with obtuse extremes.

The presence of dendritic trichomes in most of the *Sessea* species supports the separation of this genus from *Cestrum* (Benítez de Rojas & Nee, 2001) because the species of the latter genus growing in Venezuela at least do not present this type of hairs (Jáuregui et al., 2000, 2001). This character has been reported only in *Cestrum capsulare* Carvalho & Schnoor (1993/1997) (= *Sessea regnellii* Taub.) when *Sessea* was regarded as a section in *Cestrum.* Branched but not dendritic trichomes are present in *C. olivaceum* Francey, *C. strigilatum* Ruiz & Pav., and *C. tomentosum* L. f.

(Jáuregui et al., 2000). In the case of glabrate *Sessea* species, these are clearly distinguished from *Cestrum* by the presence of capsular fruit. Branched, but not dendritic, trichomes have been found in species of Solanaceae tribes Nicotianeae, Salpiglossideae, and Schwenckieae (C. de Gastiazoro, 1991, 1993, 1994). They have also been recorded in *Juanulloa ochracea* Cuatrec. (Jáuregui et al., 1997), *J. ferruginea* Cuatrec., and *J. verrucosa* (Rusby) Hunz. & Subils (Hunziker, 2001), in *Deprea orinocensis* (HBK) Raf. (Sawyer & Benítez de Rojas, 1998), and in *Solanum* spp. (Roe, 1971; Seithe, 1979; Mansilla et al., 1999). On the other hand, the presence of dendritic trichomes has been mentioned in *Solanum* spp., subsection *Cernum* (Carvalho et al., 1991), and in *Physalis peruviana* (Ganapathi et al., 1991).

Glandular hairs are common in the family Solanaceae, but they occur in different shapes.

Mixed trichomes have been reported for other species of Solanaceae, for example, some members of the tribe Anthocercideae, which contains Australian spp. (Haegi, 1991); they are also reported in some members of the tribe Schwenckieae (C. de Gastiazoro, 1994) and in *Cestrum olivaceum* Francey and *C. tomentosum* L. f. (Jáuregui et al., 2000).

Unlike Bitter, who considered only candelabra-like hairs, this report considers the occurrence of four trichome types with several subtypes, encountered in 19 studied species. For this reason, a new classification on the basis of trichome types is in preparation, including the species not considered by Bitter in his conspectus.

Trichomatic types can sometimes be related to morphologic characters that define species, for example, the pubescence of the ovary, external surface of the corolla, and stigma. This relationship cannot yet be established in all cases; the study needs to be completed for all species in order to correlate trichomatic and morphological characters that can later be used to establish groups within the genus.

The use of trichome morphology as a taxonomic criterion is particularly helpful, fast, and simple for studying herbarium specimens with leaves (Teobald et al., 1979).

CONCLUSIONS

The 19 studied species can be separated into four groups, depending on the predominance of a trichomatic type. Apart from the candelabra-like trichomes described by Bitter, which are found in high densities on the abaxial surface forming a homogeneous group from which some species can be separated by very specific characters, e.g., projections in the hair branches, three types with several subtypes are described. Likewise the trichomatic types of four species that were not considered by Bitter are described. Finally, the diagnostic value of the trichomatic types in the genus *Sessea* is demonstrated.

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The first author expresses gratitude to J. Solomon, curator of the MO herbarium, who requested loans from several herbaria, making possible her study of the genus *Sessea*; and to the staff of the Missouri Botanical Garden for their cordial hospitality and excellent facilities. We dedicate this research to the memory of W. G. D'Arcy, an impassioned specialist in the Solanaceae, friend, companion during fieldwork in Venezuela, and an inspiration to study the genus *Sessea*. Partial financial support was supplied by Consejo de Desarrollo Científico y Humanístico de la Universidad Central de Venezuela, by means of aid to research.

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NEW SPECIES IN SOLANACEAE

16

NEW SPECIES OF *CALIBRACHOA* AND *PETUNIA* (SOLANACEAE) FROM SUBTROPICAL SOUTH AMERICA

João Renato Stehmann and João Semir

ABSTRACT. We describe and illustrate three new species of Solanaceae belonging to the South American subtropical flora: *Calibrachoa cordifolia*, *Calibrachoa missionica*, and *Petunia secreta*. *Calibrachoa cordifolia* and *Petunia secreta* are endemic to the state of Rio Grande do Sul, southern Brazil; and *Calibrachoa missionica* occurs also in Rio Grande do Sul, in the province of Misiones, northeastern Argentina, and in the province of Encarnación, Paraguay.

RESUMO. Descrevemos e ilustramos neste trabalho três novas espécies de Solanaceae pertencentes à flora subtropical sul-americana: *Calibrachoa cordifolia*, *Calibrachoa missionica* e *Petunia secreta*. *Calibrachoa cordifolia* e *Petunia secreta* são encontradas no estado do Rio Grande do Sul, sul do Brasil; *Calibrachoa misionica* cresce no Rio Grande do Sul, na província de Misiones, no nordeste da Argentina e na província de Encarnación, no Paraguai.

Key words: *Calibrachoa*, *Petunia*, Solanaceae.

South America is the major center of diversity for the Solanaceae (Hunziker, 2001). Besides numerous native species from widespread genera such as *Solanum* L., *Lycianthes* (Dunal) Hassl., and *Nicotiana* L., there are more than 400 species of about 50 endemic genera, in all more than 2000 native species—an amount exceeding 70% of the specific richness of the family (D'Arcy, 1991).

Calibrachoa Cerv. ex La Llave & Lex. and *Petunia* Juss. are genera endemic to South America with centers of diversity in southern Brazil. *Calibrachoa* includes about 25 species centered in the subtropical Atlantic region of South America. The wide distribution of *C. parviflora* (Juss.) D'Arcy, which grows also in North and Central America, was considered a result of introduction (D'Arcy, 1991). This species is autogamous and could have been introduced there in the last centuries by Spanish merchants. Brazil is the richest country in species of *Calibrachoa* with 19, and the southern Brazilian plateau in Santa Catarina and Paraná can be considered the center of diversity for the genus with 13 species (Stehmann & Semir, unpublished data). *Petunia* comprises about 11 species from subtropical South America. In Brazil, 8 species grow in the southern region, while only 1 is found in the southeast. The highlands of Serra Geral in Santa Catarina (1000–1800 m altitude) can be recognized as the center of diversity of the genus. *Petunia axillaris* (Lam.) Britton, Sterns & Poggenb. and *P. integrifolia* (Hook.) Schinz & Thell., parental taxa of the garden petunia, have relatively large distributions, and both species grow in the Pampa province of southern Brazil, Uruguay, and Argentina (Wijsman, 1982). Most *Petunia* species are narrowly endemic, as for example, *P. bonjardinensis* T. Ando & Hashim., *P. exserta* Stehmann, *P. reitzii* L. B. Sm. & Downs, and *P. saxicola* L. B. Sm. & Downs.

During our studies of Brazilian Solanaceae, three undescribed species came to our attention. The new species, belonging to *Calibrachoa* and *Petunia,* are described and illustrated herein.

Calibrachoa cordifolia Stehmann & L. Aguiar, sp. nov. TYPE: Brazil. Rio Grande do Sul: Santa Maria, Reserva Biológica do Ibicuí-Mirim, no lado esquerdo da barragem Saturnino, 5 Dec. 1995, *N. Silveira 12934* (holotype, HAS). Figure 1.

Species haec *Calibrachoae ovalifoliae* proxima, a qua foliis ovatis basibus cordatis, corollis purpureis stigmatibus lobatisque recedit.

Shrub to 0.4 m high, erect or decumbent with ascendant secondary branches, trichomes 0.1–0.4 mm, simple, glandular; stem cylindrical, with woody base, grayish brown, sparsely pubescent, irregularly striate, apical stems commonly ascendant, ochraceous, pubescent; internodes 2–8 mm long; brachyblasts lacking or small, up to 3.2–4 mm long and elliptic leaves. Leaves sessile, blades 5–17 × 2–8 mm, ovate, apex acute, base cordate, more rarely rounded, margin thickened, ciliate, symmetrical, plane or slightly concave, pubescent on both sides, midrib sunken adaxially and prominent abaxially, forming a ligneous callus at the base. Inflorescence of sympodial units, each one with 1 flower associated with 2 opposite leaflike bracts; pedicels 3–9.5 mm long, pubescent; calyx 8–13 mm long, olive-green to ochraceous, externally and internally puberulent, 10-nervate, nerves thickened, cleft or lobed to the middle or more, lobes 4.5–9 mm long, unequal, triangular, apex acute; corolla funnelform, tube 8.5–11 mm long, externally with base yellow and apex magenta to purple, minutely pubescent, internally glabrous, limb ca. 15 mm diam., briefly to halfway lobed, magenta to purple, lobes 5–6 mm long, obtuse, apices abruptly acute; stamens 5, included, with 3 distinct lengths, the free portion 3 mm, 3.5 mm, and 5 mm long, the adnate portion about 3 mm long, glabrous, anthers yellow, about 0.8 mm long; nectariferous disk 2-lobed; ovary ovoid, style ca. 5 mm long, apex slightly curved, stigma shortly bilobed. Capsule 7 mm long, 4–5 mm diam., globose or ellipsoid; pedicel 9–16 mm long, deflexed; seeds 1.1–1.3 mm long, ellipsoid-reniform.

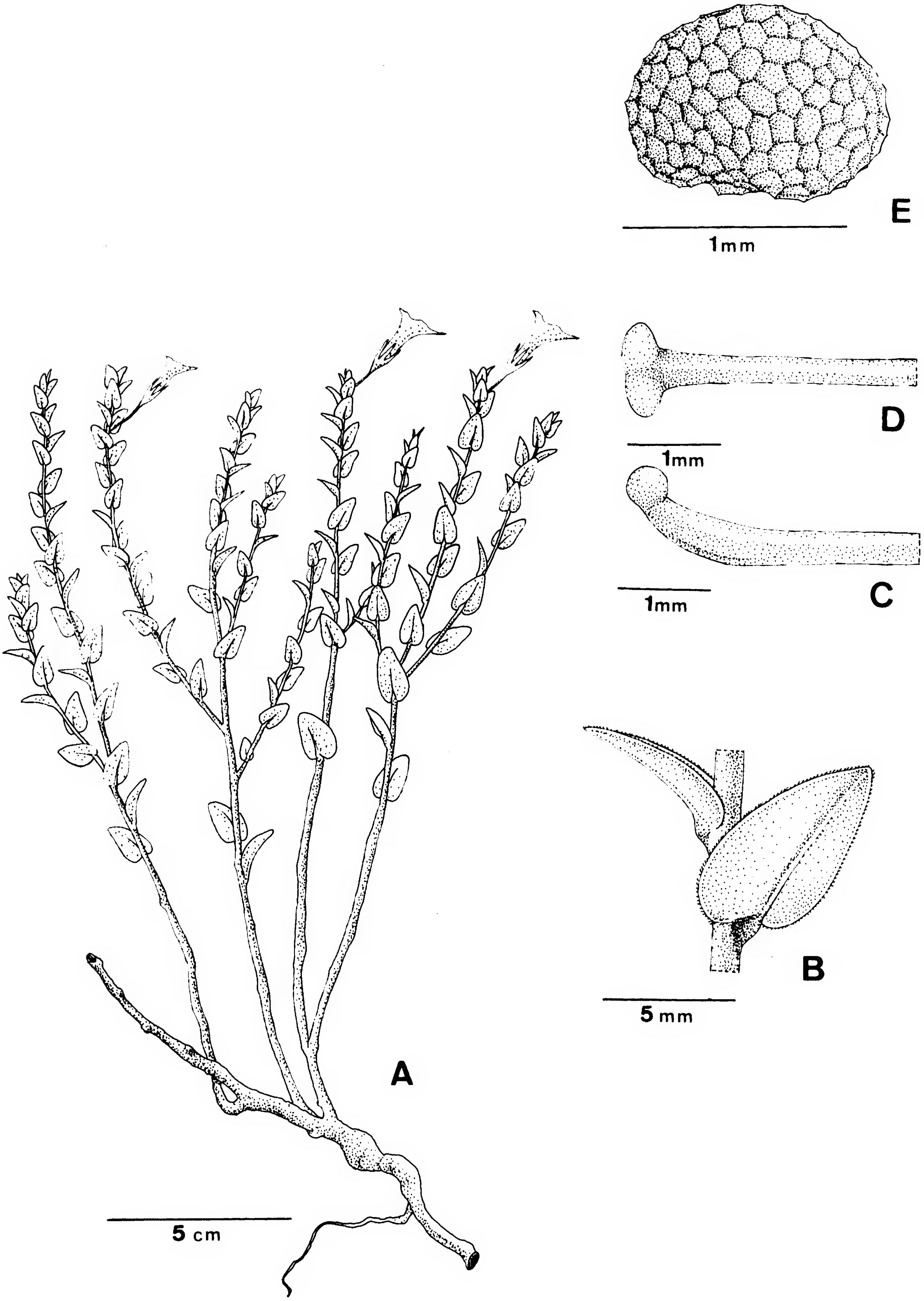

Figure 1. *Calibrachoa cordifolia* Stehmann & L. Aguiar. —A. Habit. —B. Leaf. —C, D. Apex of the style and stigma. —E. Seed. Based on the holotype, *Silveira 12934* (HAS).

Etymology. The specific epithet refers to the cordate shape of the leaves.

Distribution and habitat. Restricted to one locality in southern Brazil, in the central region of Rio Grande do Sul, at the municipality of Santa Maria, where it was collected in grasslands around the Ibicuí-Mirim reservoir, at the Reserva Biológica do Ibicuí-Mirim.

Phenology. Flowering specimens have been collected from November to December; fruiting specimens have been collected in December.

Calibrachoa cordifolia is recognized by its ligneous callus at the foliar base and nodal region of the stem, ovate leaves with cordate base, corolla magenta or purple, and bilobed stigma. The distinctly lobed stigma was a character used by Fries (1911) to differentiate some critical species of *Petunia* s.l. and is found in *C. dusenii* (R. E. Fr.) Stehmann & Semir, *C. excellens* (R. E. Fr.) Wijsman, *C. heterophylla* (Sendtn.) Wijsman, and *C. eglandulata* Stehmann & Semir.

This species was cited previously as an unidentified *Petunia* by Aguiar et al. (1998), who indicated that it was probably new and related to *Petunia ovalifolia* Miers [= *C. ovalifolia* (Miers) Stehmann & Semir] and *P. excellens* R. E. Fr. [= *Calibrachoa excellens*].

Calibrachoa cordifolia morphologically resembles *C. ovalifolia*, because both species have a prominent ligneous callus at the base of the midrib and nodal region of the stem. The callus is persistent and can be easily observed at all nodes. *Calibrachoa ovalifolia* can be distinguished from *C. cordifolia* by its elliptic or ovate leaves with rounded bases, and corolla limb whitish to pink, with a yellow, violet net-veined throat.

Calibrachoa excellens is widely distributed in southern Brazil and occurs sympatrically with *C. cordifolia* at the Reserva Biológica do Ibicuí-Mirim. Both species have a bilobed stigma and magenta corolla limb, but *C. excellens* can be easily distinguished by its elliptic leaves with an attenuate or rounded base, lacking the callus.

Paratype. BRAZIL. **Rio Grande do Sul:** Santa Maria, Res. Biol. do Ibicuí-Mirim, barragem Saturnino de Brito (CORSAN), 8 Nov. 1988, *N. Silveira 5962* (HAS, UEC).

Calibrachoa missionica Stehmann & Semir, sp. nov. TYPE: Brazil. Rio Grande do Sul: Santo Ângelo, 29 Sep. 1976, *K. Hagelund 10424* (holotype, ICN). Figure 2.

Species haec affinis *Calibrachoae ovalifoliae,* a qua nodis caulium et basibus costae foliorum ecallosis, corollisque magentis vel purpureis recedit.

Decumbent shrub to 0.4 m high, pubescent or pilose, trichomes 0.2–0.5 mm long, simple, glandular; stems profusely branched, basally ligneous, longitudinally striate, pubescent; internodes 2.8–13 mm long; brachyblasts usually absent, sometimes present on basal nodes, 3–4 mm long. Leaves sessile, (6)9–22 × 2.5–7 mm, obovate or elliptic, more rarely ovate, apex acute or obtuse, base cuneate, margin thickened, surface plane, symmetric or slightly asymmetric, pubescent, ochraceous, midrib sunken adaxially and slightly prominent abaxially, not thickened at base. Inflorescence of sympodial units, each one with 1 flower associated with two opposite leaflike bracts; pedicels 6.5–15 mm long, pubescent or pilose; calyx 8–9.5 mm long, 10-nerved, halfway or more cleft-lobed, lobes 4.5–5.5 mm long, narrow-triangular, lanceolate or subulate, apices acute; corolla funnelform, tube 8–11 mm long, limb 14–20 mm diam., magenta or purple, lobes obtuse, abruptly acute; stamens 5, with three distinct lengths, the free portions 2–2.8 mm, 2.9–3.4 mm, and 4.4–4.6 mm long, the adnate portions 2.5–3.3 mm, longer filaments glabrous or with apex minutely pubescent, included, anthers yellow, about 0.8 mm long; nectariferous disk 2-lobed; ovary 1.1–1.5 mm long, ovoid or narrow-obconic, style 5.3–6 mm long, thickened at apex, stigma 0.7–0.8 mm long, elliptic, shortly bilobed. Capsule 5–7.7 mm long, 3.5–3.7 mm diam., ovoid; pedicel 6.6–20 mm long, curved, deflexed; seeds ca. 0.8 mm long, globose-ellipsoid.

Etymology. The specific epithet refers to the geographic area of distribution, known as Missões in Brazil and Misiones in Argentina.

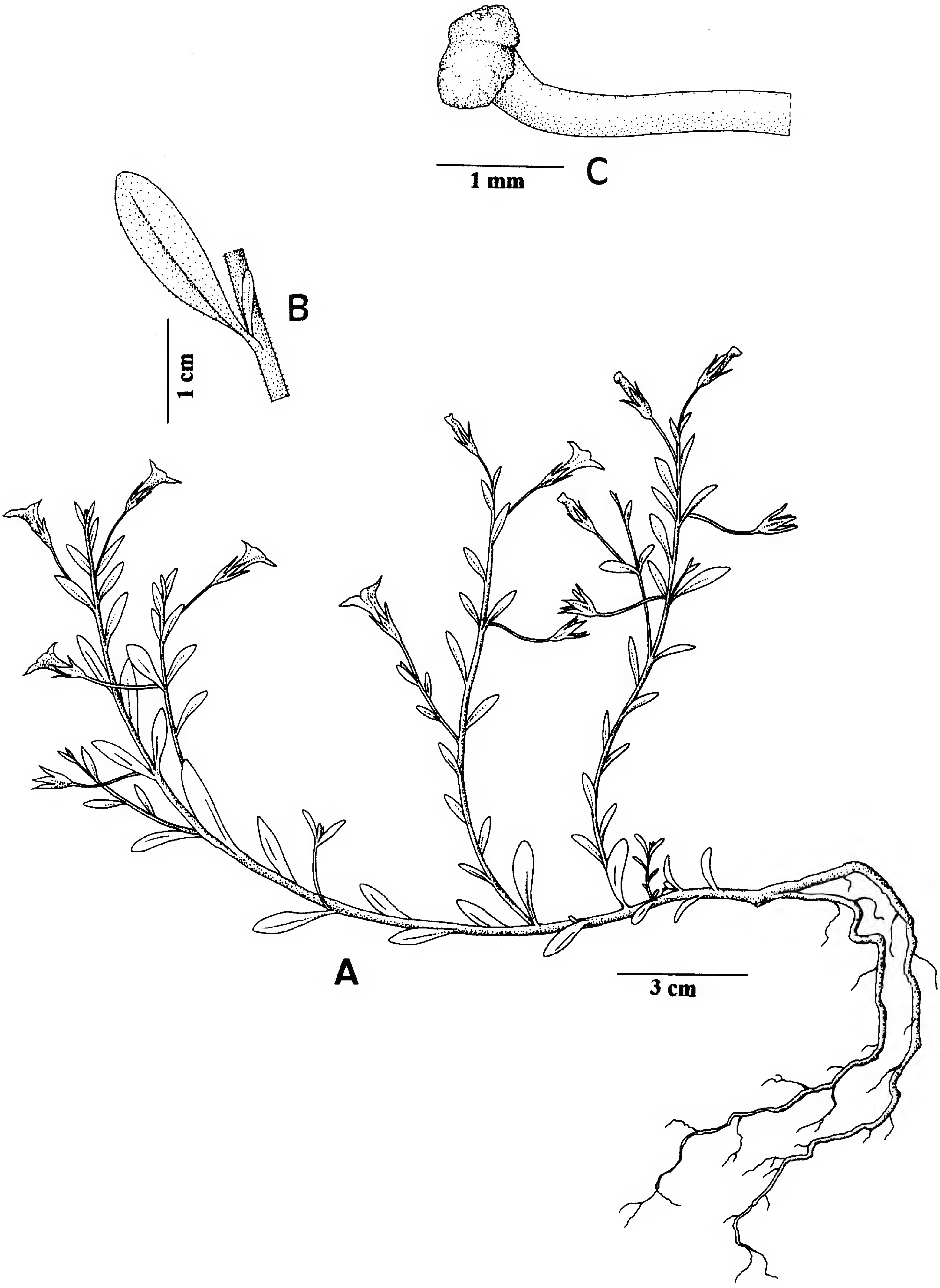

Figure 2. *Calibrachoa missionica* Stehmann & Semir. —A. Habit. —B. Leaf. —C. Apex of the style and stigma. Based on the holotype, *Hagelund 10424* (ICN).

Distribution and habitat. Calibrachoa missionica occurs in southern Brazil (northeastern Rio Grande do Sul), Paraguay (Encarnación), and Argentina (Misiones and Corrientes). It inhabits rocky places.

Phenology. Flowering and fruiting specimens have been collected from August to October and February to April.

Calibrachoa missionica is characterized by its decumbent habit, elliptic leaves lacking a callus at the base of midrib on the abaxial surface, and its purple, short-funnelform corolla, with the calyx slightly shorter than the corolla tube.

This species is similar to *C. ovalifolia*, and several collections of *C. missionica*, especially those from Argentina, have been determined previously as *Petunia helianthemoides* Sendtn. and *P. calycina* Sendtn. [= *C. ovalifolia* (Miers) Stehmann & Semir]. The presence of a prominent callus at the nodes and the base of the midrib on the abaxial surface of the leaves and the whitish or pink corolla in *C. ovalifolia* permit one to distinguish it from *C. missionica.*

The only two Brazilian collections of *C. missionica* were obtained in northwestern Rio Grande do Sul, at the region called Missões, bearing few flowers and fruits. This region was originally covered by subtropical semi-deciduous forest and grasslands, but in the last three decades the landscape has been changed as a consequence of the annual cultures. There are no recent collections of this species in Brazil, and for this reason it is important to locate new populations and to check its conservation status.

Paratypes. ARGENTINA. **Misiones:** Candelaria, Martires, 8 Oct. 1947, *Bertoni s.n.* (B, W); Cainguás, Puerto Mineral, *G. J. Schwartz 10682* (G); Corpus, *Bertoni 1873* (W); Iguazu, Eldorado, *E. Schwindt 2206* (W p.p.), 27 Sep. 1949, *E. Schwindt 2128* (G); Posadas, "loco glareoso saxoso pr. praedium la Granja frequens," *E. L. Ekman 861* (G, US); San Ignácio, *J. E. Montes 1908* (K, US); Balsa Ñancanguazú, 1945, *G. W. Schwartz 1192* (W); Arroyo Bucre Grande, *G. J. Schwartz 2062* (E); Puerto Nuevo, *G. J. Schwartz 2200* (BR); Santa Maria, *G. J. Schwartz 2503* (G); Santo Pipó, *G. J. Schwartz 4864* (W), *G. J. Schwartz 6356* (G); Oasis, *G. W. Schwartz 10567* (W), *B. R. Medina 45* (E, G); Santa Ana, *J. E. Montes 1066* (K), *A. de Llamas 438* (G), *A. de Llamas 472* (G); locality not indicated, *E. Hassler 511* (G), *E. Hassler 512* (G), *E. Hassler 513* (G). **Corrientes:** General Paz, Puissoye, *T. S. Ibarrola 3649* (B, BR, W); Ituzaingó, *M. M. Arbo, S. G. Tressens, A. Schinini & S. Ferrucci 2126* (K). PARAGUAY. **Encarnación:** Itauna, 150 m, *Bertoni 4493* (W).

Petunia secreta Stehmann & Semir, sp. nov. TYPE: Brazil. Rio Grande do Sul: Caçapava do Sul, Pedra do Segredo, 2 Nov. 1995, *J. R. Stehmann 2101, J. Semir & J. Dutilh* (holotype, UEC; isotypes, BHCB, MO). Figure 3.

Petuniae axillari valde affinis, sed corollis constanter purpureis distincta.

Annual herbs to 1 m high; trichomes 0.4–1.2 mm long, simple, glandular; stems with one erect axis or later producing basal ascendant secondary branches, cylindrical, longitudinally striate, pilose; internodes 5–35 mm long, shorter toward base and longer apically. Leaves basally rosulate, crowded, late senescent, apically more sparse, 70–110 × 15–40 mm, spathulate or oblanceolate, sometimes deltoid, acute at apex, long-attenuate at base, decurrent on a winged petiole, pilose, midrib evident, secondary nerves 3 or 4 pairs, the first 2 pairs rising near the base. Inflorescence with numerous sympodial units, each one composed of 1 flower associated with 2 opposite leaflike bracts; bracts ovate or elliptic, with base short-attenuate, rounded or subcordate; internodes 15–50 mm long, generally longer than vegetative ones, pilose. Flowers not fragrant; peduncle 14–55 mm long, pilose; calyx deeply lobed, tube 3–5 mm long, lobes 10–15 mm long, narrow-oblong to narrow-oblanceolate, apex acute or obtuse; corolla actinomorphic, salverform, tube 38–48 mm long, subcylindrical, externally striate, throat yellowish green, limb 2.8–3.5 mm diam., purple, shortly lobed, lobes obtuse, with apex retuse; stamens 5, 4 long and 1 short, filament of the long stamens 4–4.7 mm long, subequal, filament of the short stamen 3.7–4 mm long, adnate for half its length, anthers yellow, slightly included, opening close to the mouth of the corolla tube; ovary 4–5 mm long, narrow-ovoid, style 4–4.1 cm long, stigma globose-dilated, located slightly above the anthers. Capsule 9–17 × 6–8 mm, ovoid, calyx with enlarged lobes, almost twice the length of the capsule; pedicel 24–40 mm long, inflexed; seeds 0.43–0.49 mm long, subglobose. Chromosome number $2n = 14$.

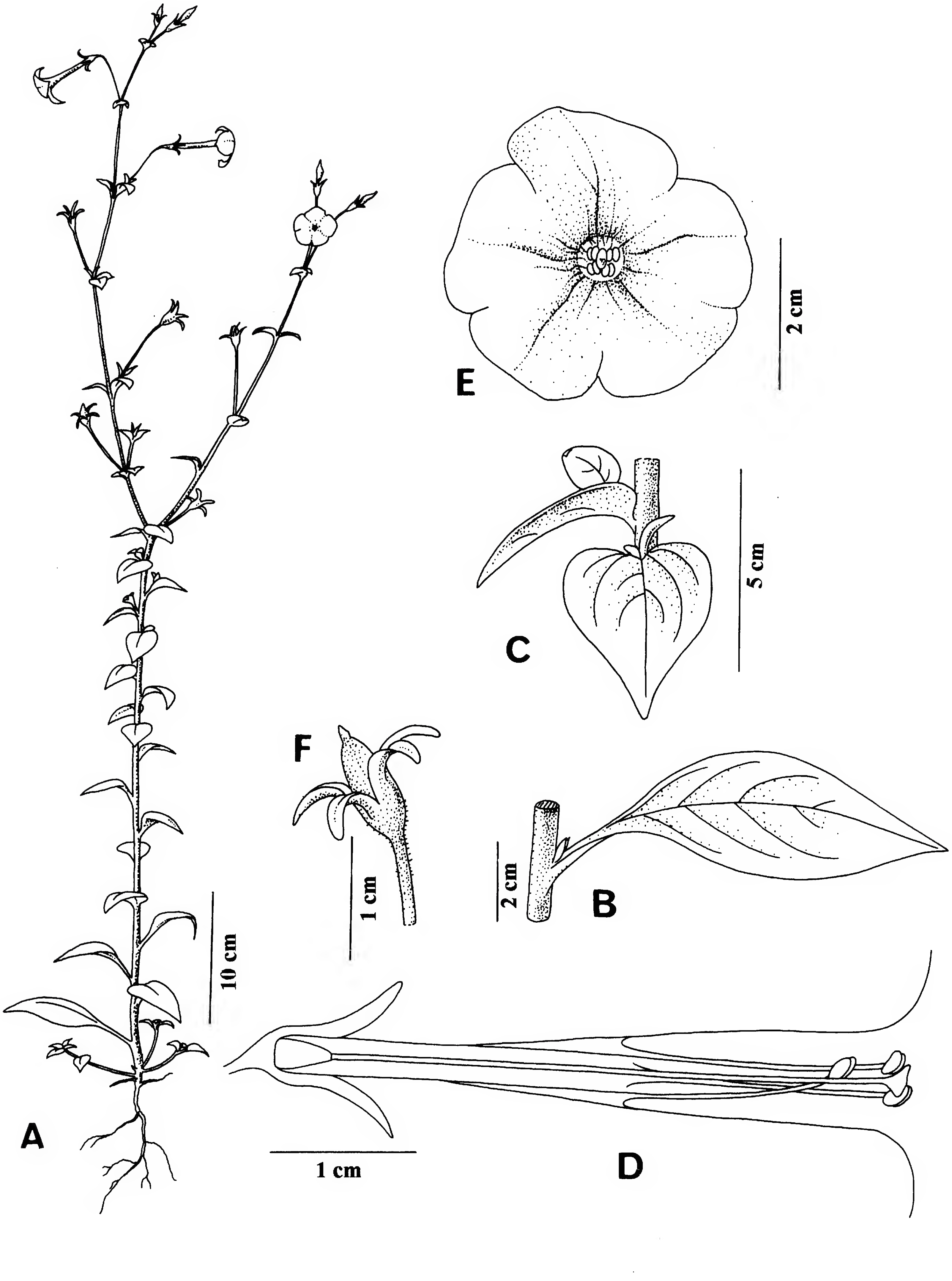

Figure 3. *Petunia secreta* Stehmann & Semir. —A. Habit. —B. Basal leaf. —C. Apical leaf. —D. Flower in longitudinal cross section. —E. Corolla limb. —F. Immature capsule. Cultivated specimen at UEC: progeny of the holotype, *Stehmann 2101 et al.*

Etymology. The specific epithet is a reference to "Pedra do Segredo" (Rock of the Secret), a mysterious place in the municipality of Caçapava do Sul, where this species is hidden.

Distribution and habitat. Petunia secreta is endemic to the place called "Pedra do Segredo," at the municipality of Caçapava do Sul, in Rio Grande do Sul, southern Brazil. It is clearly heliophilous, inhabiting the top of conglomerate sandstone towers at about 300–400 m elevation.

Phenology. Flowering specimens have been collected from November to January, and fruiting specimens from December to January.

Petunia secreta is an annual herb, erect or ascendant, easily recognizable by its purple and salverform corolla. *Petunia secreta* and *P. axillaris* are similar morphologically, and the color of the corolla is the unique consistent character distinguishing them. *Petunia axillaris* can be recognized by its white flowers, while *P. secreta* has purple flowers. In dried herbarium material, purple flowers of *P. secreta* turn bluish, but the white flowers of *P. axillaris* do not change color. The length of the corolla tube is equivalent to that described for *P. axillaris* subsp. *axillaris*, not exceeding 50 mm long, while the stamens arranged in two different sizes (4+1) resemble the androecium of *P. axillaris* subsp. *parodii* (Steere) Cabrera. The two infraspecific taxa of *P. axillaris* seem to be allopatric to each other (Ando, 1996), and in the region of Caçapava do Sul only *P. axillaris* subsp. *parodii* occurs.

Besides these morphological characters, we observed distinctive features also related to pollination. The flowers of *P. secreta* have no perceptible fragrance and were visited by small bees (Halictidae, *Pseudagapostemon* Schrottky), while those of *P. axillaris* are sweetly fragrant in the evening and pollinated by hawkmoths (Sphingidae, *Manduca* Hübner) (Galetto & Bernardello, 1993; Ando et al., 2001). Natural hybrids between both species could not be found in the region.

Paratypes. BRAZIL. **Rio Grande do Sul:** Caçapava do Sul, Pedra do Segredo, *J. R. Stehmann 1209, J. H. A. Dutilh & A. Sciamarelli* (UEC); Pedra do Segredo, *J. R. Stehmann 1213, J. H. A. Dutilh & A. Sciamarelli* (UEC); Pedra do Segredo, *J. R. Stehmann 1234, J. H. A. Dutilh & A. Sciamarelli* (UEC); Segredo, *J. R. Stehmann 1318, A. O. Vieira & D. Falkemberg* (UEC).

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17

A NEW SPECIES OF *CHAMAESARACHA* (SOLANACEAE)

John E. Averett

ABSTRACT. *Chamaesaracha darcyi* is described as a new species. The taxon has a dense indument of dendritic hairs on the leaf and stem that distinguishes it from other species of the genus. The species also has a more eastern range than any of the other species of *Chamaesaracha*. The chromosome number of the species is newly published here. Recognition of this taxon will help clarify variation and interspecific relationships, especially between the problematic species *C. coronopus* A. Gray and *C. coniodes* (Moric. ex Dunal) Britt., which it most closely resembles.

Key words: *Chamaesaracha,* Solanaceae.

Chamaesaracha coronopus and *C. coniodes* are highly variable species. The two are sympatric throughout much of their range and, in some instances, can be quite similar. They are distinct in the western part of their range, but plants from populations in southern Texas and adjacent Mexico are easily confused. *Chamaesaracha darcyi* is most similar to *Chamaesaracha coniodes*, especially in habit and leaf shape. Indeed, specimens of this taxon were included in the latter species in an earlier revision of the genus (Averett, 1973). The latter species, however, lacks the dendritic-stellate trichomes of the leaves and stems, usually having instead simple trichomes mixed with glandular hairs.

Chamaesaracha darcyi Averett, sp. nov. TYPE: U.S.A. Texas: Palo Pinto Co., near Lake Possum Kingdom along hwy. 36, 27 June 1969, *Averett & Bierner 474* (holotype, TEX).

Chamaesarachae coniodi similis sed trichomatibus dendritici-stellatis et distributione geographica orientaliore differt.

Plants perennial herbs, rhizomes subligneous to woody, stems prostrate to ascending, 10–30 cm long; leaves broadly lanceolate to ovate-lanceolate, pinnatifidly lobed, 2.5–5.0 cm long, 1.0–2.0 cm wide, densely pubescent with dendritic trichomes; flowers 1 to 2 in axils, pedicel 2.0–3.5 cm long, calyx ca. 4.0 mm high; corolla cream-white, 1.0–1.5 cm wide; fruit ca. 7 mm diam.; seeds rugose-reticulate, ca. 3.0 mm long and 2.0 mm wide; chromosome number, $n = 24$.

Chamaesaracha darcyi is found in the Rolling Plains of northern Texas, but extends east into the Cross Timber and Prairies regions of Texas and north into southwestern Oklahoma. The new species occurs in grasslands and has the most northeastern distribution of any species of *Chamaesaracha*. *Chamaesaracha darcyi* is named in honor of William G. D'Arcy, a student of the Solanaceae and a long-time friend.

Chamaesaracha is an exceptionally close-knit group of taxa, and essentially all of the species have been confused (Averett, 1973). The three species discussed here are particularly difficult. All are typically tetraploid, $n = 24$, and are sympatric in parts of their ranges.

Pubescence is an important character in a number of genera in the Solanaceae (Roe, 1971; Seithe & Sullivan, 1990) and is one of the more reliable characters in distinguishing the species of *Chamaesaracha* (Averett, 1973). Leaf and stem pubescence is reasonably consistent within a species but generally must be used in combination with leaf shape. For example, stellate or dendritic hairs are found in *C. coronopus*, but there the leaves are linear-lanceolate, typically 4–10 times longer than wide. The leaves of *C. darcyi* are similar to those of *C. coniodes*, ca. 1.5–2 times longer than wide, but the latter has simple (rarely branched) trichomes mixed with glandular hairs. The combination of leaf shape, pubescence, and distribution of *C. darcyi* is unique and distinctive within the genus.

ACKNOWLEDGMENTS

I thank Guy Nesom for assistance with the Latin diagnosis and B. L. Turner for reviewing parts of the manuscript. I also thank Richard Keating and James Solomon for looking through specimens at MO for additional type material.

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SYSTEMATICS AND NEW SPECIES OF VARIOUS FAMILIES

18

A NEW ENDEMIC SPECIES OF *ANTHURIUM* (ARACEAE) FROM PANAMA

Thomas B. Croat

Abstract. *Anthurium darcyi* Croat, a member of section *Calomystrium*, is described from Panama, Province Panamá. The species does not resemble any other species in Central America, and is compared with *A. cogolloanum* Croat, from Colombia.

Key words: *Anthurium*, Araceae, new species, central Panama.

Anthurium darcyi Croat, sp. nov. TYPE: Panama. Panamá: Comarca de San Blas, Cerro Brewster, 850 m, 9°18'N, 70°16'W, 20 Nov. 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6285* (holotype, MO-3320651-4; isotype, PMA). Figures 1, 2.

Planta epiphytica vel terrestris; internodia brevia; cataphylla persistentia semi-intacta, 45–50 cm longa; petiolus 75–180 cm longus, multi-angulatus in sicco; lamina ovato-cordata, 80–105 cm longa, 50–60 cm lata; sinus spathulatus, 20–23 cm profundus; nervi primarii laterales 8 utroque; pedunculus 30–32 cm longus; spatha 17–19 cm longa, 3.5–4 cm lata, viridis; spadix cylindroideus, 20–30 cm longus, 2–3 cm diam., albus per anthesin.

Epiphytic or terrestrial; stems erect, short, ca. 10 cm diam.; internodes short; cataphylls persisting semi-intact, 45–50 cm long, 10–12 cm wide, with the epidermis drying brown[1] (B & K yellow 4/7.5), often with a mass of yellowish longitudinal fibers; leaves with petioles erect-spreading and blades somewhat pendent; petioles 75–180 cm long, 6–11 mm diam., flattened to broadly sulcate adaxially with prominent marginal ribs and a usually smaller medial rib, usually 3-ribbed adaxially, with additional smaller ribs around the circumference (up to a total of 10 ribs around the circumference including the 3 larger abaxial ribs), drying sharply many-angular, the surface brownish (same as cataphylls); geniculum ca. 1.6 cm long, drying darker than petiole, the ridges on the geniculum undulate; blades ovate-cordate, 80–105 cm long, 50–60 cm wide, 1.6 times longer than wide, broadest at point of petiole attachment, prominently lobed at base, acuminate to abruptly acuminate at apex; the margins broadly convex and undulate; anterior lobe 60–75 cm long, broadest near the base; the posterior lobes 25–30 cm long, 20–25 cm wide, directed toward the base then prominently curved inward, sometimes overlapping; sinus spathulate to oval, 20–23 cm deep; upper surface dark green and semiglossy, matte on drying, green-brown with conspicuous, punctiform whitish cellular inclusions; lower surface drying semiglossy and green-brown or brown with dense, minute dark markings and much larger punctiform gland-like dark projections; midrib prominently and acutely raised above, thicker than broad to prominently round-raised and winged below, drying darker than surface; basal veins 7 to 9 pairs, the 1st and 2nd, sometimes the 3rd, free to the base; the 4th to 5th and higher coalesced 4.5–7 cm, the remainder coalesced 2–3 cm; posterior ribs curved, prominently raised below, naked 8–10 cm along sinus; primary lateral veins 7 to 8 per side, departing midrib at 30–45° angle, ± straight to the margin in the lower part of the blade, more arcuate in the upper 1/3 of the blade, weakly quilted-sunken above, prominently and acutely raised to knife-edged, drying darker than surface below; interprimary veins almost as prominent as primary lateral veins; tertiary veins drying prominently raised below, prominulous above; reticulate veins visible on drying; collective veins arising from one of the lowermost basal veins, weakly raised on both surfaces, 1–5 mm from the margin. Inflorescence pendent, peduncle 30–32 cm long, 0.8–1.0 cm diam., shorter than the petioles, drying brown, terete, pendent, weakly ribbed circumferentially with pale cellular inclusions; spathe 17–19 cm long, 3.5–4 cm wide, green, narrowly acuminate at apex (acumen to 2 cm long); spadix with stipe 15–23 mm long in front, 6–10 mm long in rear, cylindroid, 20–30 cm long, 2–3 cm diam. midway, weakly tapered toward both ends but mostly toward the apex, slightly curved, white at anthesis, becoming yellow to yellowish brown post-anthesis, drying brown; flowers square, 1.2–2.5 mm wide in both directions, 25 to 40 flowers visible in principal spiral, 40 to 80 flowers visible in the alternate spiral; tepals drying matte, lateral tepals 0.5–0.7 mm wide, their inner margins slightly concave, the outer margins 2-sided,

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[1] Colors are based on a Berlin and Kay Munsell Color Chart (Berlin & Kay, 1969). It is a reproduction of the Munsell Color Array of 40 hues, at maximum saturation with nine degrees of brightness in horizontal rows. Colors are arranged in 10 basic clusters of 4 different hues per cluster, ranging from red through yellow, green, blue-purple, and red-purple. The four columns for each cluster are numbered 2.5, 5, 7.5, and 10 and are repeated for each basic color type. The colors are read by stating first the color group, followed by the row, and then the column.

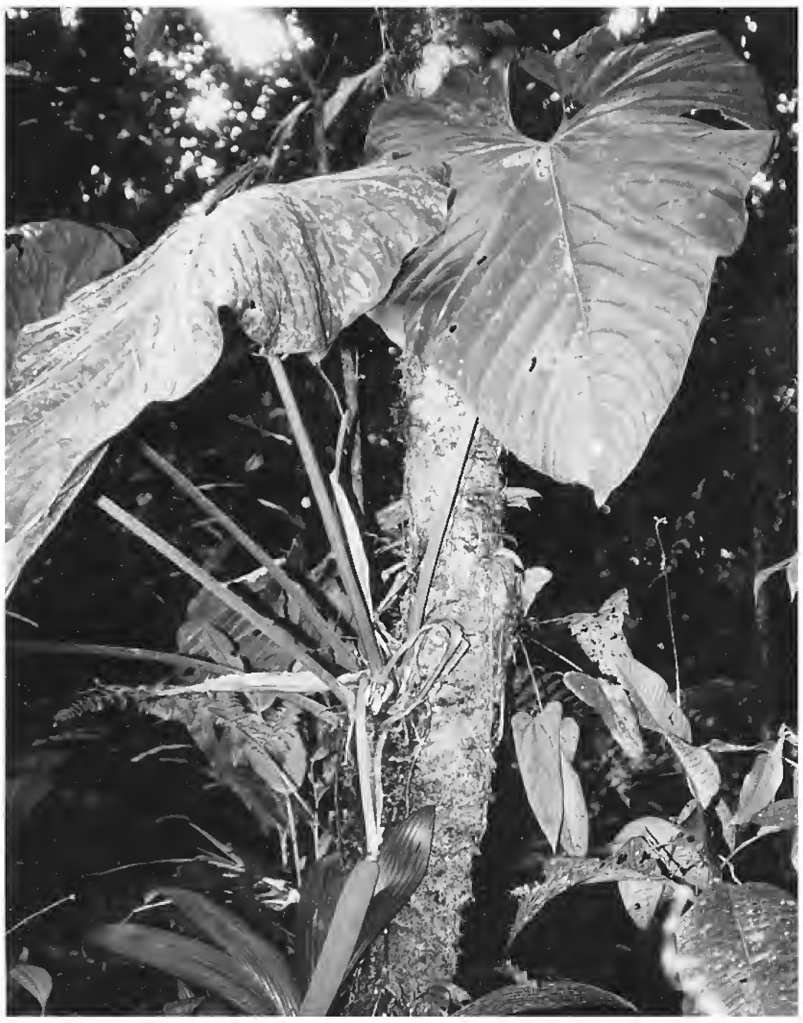

Figure 1

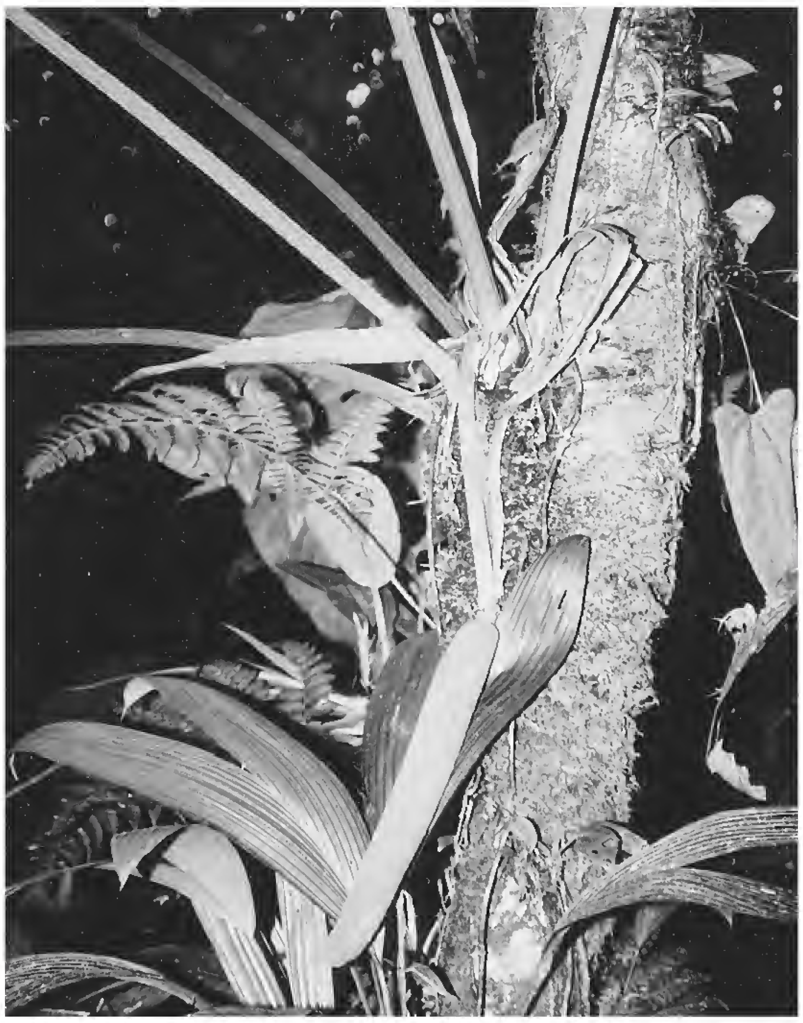

Figure 2

Figures 1, 2. *Anthurium darcyi* Croat *(de Nevers et al. 5542).*—1 (left). Habit, showing plant attached to tree with erect leaves and pendent inflorescence.—2 (right). Stem with erect-spreading petioles and pendent inflorescences. Photo credits: Barry Hammel.

straight to weakly convex; pistils exserted, drying semiglossy; stigma circular to oblong, 0.3–0.5 mm long, depressed medially, the style conspicuous; anthers drying orange.

Anthurium darcyi is endemic to Panama and known only from Cerro Brewster, where it is believed to be restricted. The species was first collected on 25 April 1985 on an expedition by Greg de Nevers, Heraclio Herrera, Barry Hammel, and Susan Charnley on their first trip to Cerro Brewster, an isolated peak about a day's walk from Cerro Jefe. The species was first discovered on that expedition by Barry Hammel, whose keen eye for differences has yielded many novelties in Araceae, but he has already been honored with two other species of *Anthurium*. The second known and designated type specimen of *Anthurium darcyi* was collected in the same region on a second trip made by Greg de Nevers, A. Henderson, H. Herrera, G. McPherson, and L. Brako.

The species is characterized by its large ovate-cordate blades, multiribbed petioles, and spindle-shaped white spadix. It is not confused with any other species in Central America. It is a member of section *Calomystrium*, defined by persistent, intact cataphylls and the presence of gland-like dots on the lower leaf blade surface. *Anthurium* sect. *Calomystrium* is a group renowned for colorful inflorescences and fragrant flowers, though *A. darcyi* is unusual for that section in having conspicuously ridged petioles.

Anthurium darcyi has no known close relatives in Central America but vaguely resembles *A. cogolloanum* Croat from Chocó Department, Colombia. That species has blades ovate-triangular and 1.8–2 times longer than broad (vs. ovate-cordate and 1.6 times longer than broad in *A. darcyi*), conspicuously quadrangular petioles (vs. terete and multiribbed), and a 66–93 cm long peduncle with purplish violet to maroon long-tapered spadix (vs. a short-pedunculate cylindroid white spadix).

The type locality of *Anthurium darcyi* is unusual in being one of three regions of premontane rainforest just east of the Panama Canal, but the only one that remains poorly explored owing to the fact that there are no roads anywhere near the region and getting there is about an 8-hour hike over rough, undulating terrain. The other two regions of premontane rainforest, namely the Cerro Jefe Region on the Pacific slope and the Santa Rita Ridge area on the Atlantic slope, are renowned for the percentages of the flora that are endemic. Judging from the number of endemic species of Araceae brought back by non-specialists, Cerro Brewster is probably going to prove to be another region of high endemism for Araceae. Another of the few collections brought back by one of the two expeditions to this area has proven to be a new species of *Syngonium*.

The species described here is named in honor of the late William D'Arcy, whose role in completing the *Flora of Panama* cannot be overestimated. Bill D'Arcy began working on the *Flora of Panama* while doing his thesis on the Solanaceae of Panama in the late 1960s. Later he wrote other families for the *Flora of Panama* while it was under the supervision of Duncan Porter. He continued this work on the *Flora of Panama* after the Garden received a 5-year NSF award and I was put in charge of the project in 1972. D'Arcy finally took charge himself when I received independent NSF funding to work on the Araceae of Central America. He was the last principal investigator for the project and the one who brought the *Flora of Panama* to its completion.

From my earliest years at the Garden I had been involved with collecting for the *Flora of Panama* and have warm memories of our days spent in the field together, both when he was a graduate student working on Solanaceae and later while we collaborated on the *Flora of Panama*. While we could never agree about where to collect (his preferences were the weedier areas where Solanaceae predominate and mine were the tracts of wet virgin forest where Araceae reigned supreme), he remained my closest friend. His unparalleled skills at organizing and planning partly stemmed from his earlier training as an economist and his stint as a business operator in the West Indies. His accomplishments in completing the *Flora of Panama* and in organizing the superb symposium in Panama that celebrated its completion make him a worthy namesake for this beautiful and rare cloud forest *Anthurium*.

Paratype. PANAMA. **Panamá:** Comarca de San Blas, Cerro Brewster, 9°18′N, 79°16′W, 850 m, 25 Apr. 1985, *de Nevers et al. 5542* (MO).

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19

EUGENIA DARCYI (MYRTACEAE), A NEW SPECIES FROM THE LOW-ELEVATION CLOUD FORESTS IN CENTRAL PANAMA

Fred R. Barrie

Abstract. A new species, *Eugenia darcyi*, is described from central Panama. Similar to *E. austin-smithii* Standl., it differs most significantly in having branches with knobby nodes, smaller flowers, and obovoid or ellipsoid fruits with a thin pericarp. It is apparently endemic to the low-elevation cloud forests (ca. 500–1000 m) that exist on isolated peaks and ridges in the region.

Key words: *Eugenia,* Myrtaceae, Panama.

Neotropical cloud forests have long been recognized as areas rich in endemic species. In central and eastern Panama, cloud forest communities occur on isolated peaks and ridges between 500 and 1000 m, elevations much lower than for cloud forests elsewhere in Central America (Myers, 1969). These lower elevation cloud forests are home to many taxa not found elsewhere (Lewis, 1971).

The new species described below was discovered while revising *Eugenia* for the *Flora Mesoamericana* Project. All but one of the known collections are from the cloud forest of Cerro Jefe (elev. ca. 1000 m), a site that has proven a particularly productive source of new taxa (Dwyer, 1967; Mickel, 1992; Barrie, 2004).

Eugenia darcyi Barrie, sp. nov. TYPE: Panama. Panamá: Cerro Jefe area, near Altos de Pacora, 600–950 m, 19 Feb. 1981, *W. G. D'Arcy & K. Sytsma 14750* (holotype, MO). Figure 1.

Differt a *Eugenia austin-smithii* statura minore, ramulis nodosis et floribus minoribus dimidio.

Shrubs or small trees, typically 3 m or less; young growth sparsely to moderately appressed-pubescent with coppery, dibrachiate hairs. Branchlets initially reddish and compressed, soon terete and glabrate, with knobby nodes and gray, exfoliating bark. Leaves elliptic, the blades 5–12 × 2.5–6 cm, 1.5–2.5 times as long as wide, coriaceous, the upper surface drying dark and glossy, the lower surface duller and somewhat lighter in color; midvein depressed above, raised and tapering distally below; lateral veins raised on both surfaces, 8 to 10 per side, ascending with a slight upward curve, interconnected by numerous, prominent netted veins; marginal veins similar to the lateral veins and straight or very weakly arched between them, 1–2 mm from the margin; the upper surface and midvein soon glabrate, the lower surface and midvein glabrate or with a few, persistent dibrachiate hairs near the base; younger leaves may have numerous, small glands on both surfaces, these typically obscure in mature leaves; base cuneate to obtuse or rounded; margins decurrent along the petiole; apex abruptly acuminate or obtuse with a small, bluntly acute tip; petioles 5–10 mm, glabrate or with scattered, appressed dibrachiate hairs, depressed or sulcate dorsally. Inflorescence cauliflorous, fasciculate, flowers 2 to 6, possibly more; bracts persistent, elliptic, minute, less than 0.5 mm long in flower and becoming extremely reduced in fruit; buds not seen. Flowers pedicellate, the pedicels 2–8 mm, glabrous or with a few appressed hairs; bracteoles adnate to the hypanthium or dilated at anthesis, ovate, 0.5 × 0.5 mm, glabrous, the pair slightly fused at the base but not forming a well-defined involucre, the margins scarious, the apex acute; hypanthium obconic, 1–1.5 mm, glabrous; calyx lobes in unequal pairs, the outer pair 1.5–2 × 2 mm, the inner pair 2–2.5 × 2 mm, ovate and concave, reflexed at anthesis, the margins ciliate, the apex rounded; petals ovate, 3–3.5 × 2 mm, the margins ciliate, the apex rounded; disk 1.5–2.5 mm diam., uniformly covered with erect, coppery hairs, these ca. 0.3 mm; stamens ca. 50, 2–3 mm; anthers 0.5 mm; style 3–4 mm, glabrous; ovule number ca. 16. Fruits obovoid or ellipsoid, 20–30 × 10–20 mm, the base attenuate, thin-walled, glabrous, glandular, with up to 8 poorly defined vertical ridges; immature color red, mature color black or purple-black.

Distribution. Cloud forest zone on Cerro Jefe and similar habitats in Coclé Province, 500–1000 m.

Phenology. Flowering September–October; fruiting October–June.

Specimens of *Eugenia darcyi* have been previously identified as *E. austin-smithii* Standl., a montane forest species of western Panama and Costa Rica. In Panama, *E. austin-smithii* occurs in Chiriquí and Bocas del Toro at elevations of 1300–1600 m. The leaves of the two species are similar, although those of *E. darcyi*

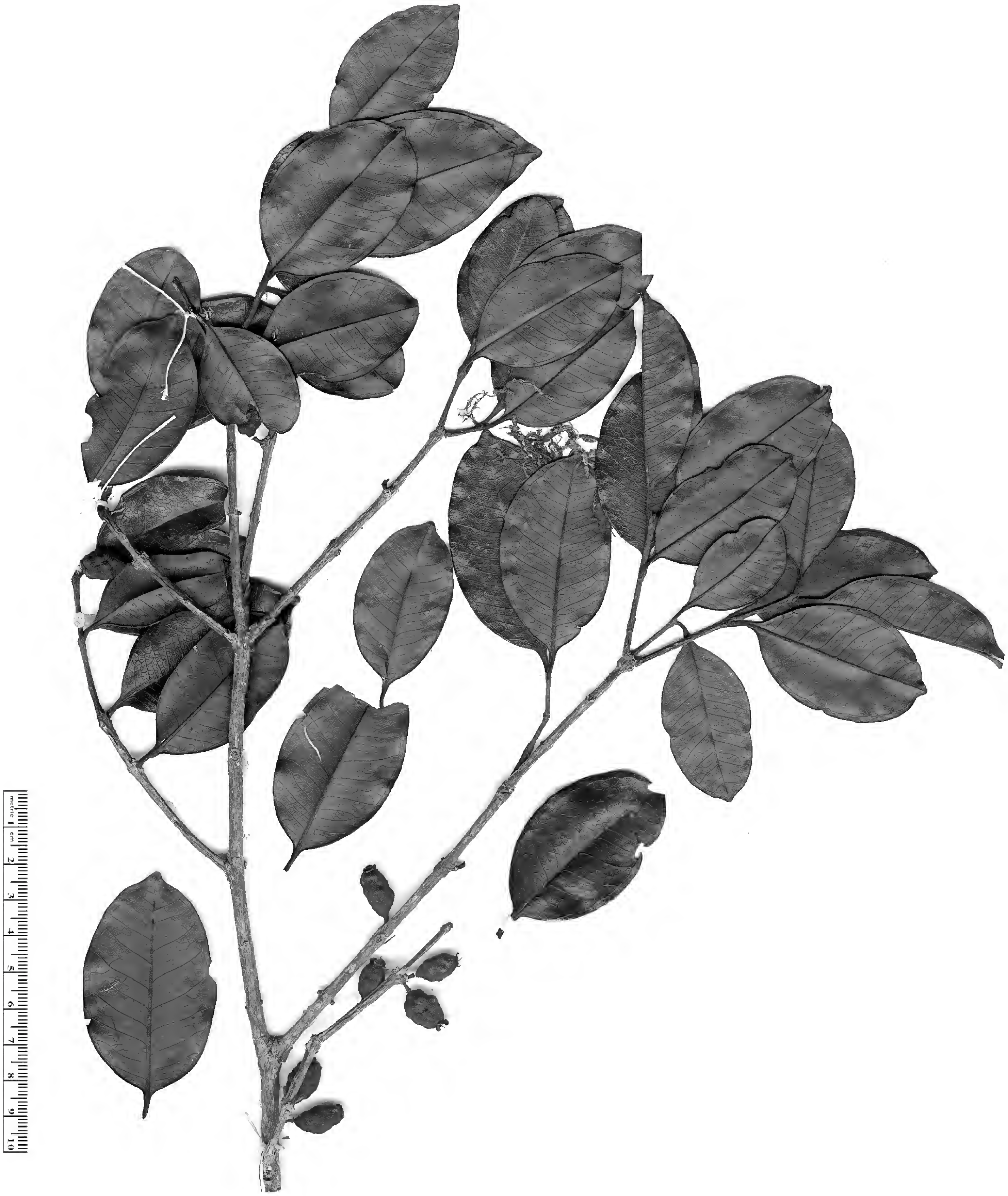

Figure. 1. Holotype of *Eugenia darcyi, D'Arcy & Sytsma 14750* (MO).

tend to be glossier. The two differ in many respects, however. *Eugenia darcyi* is a shrub or small tree of about 3 m, while *E. austin-smithii* is a much larger tree, reaching heights of 20 m or more. The young growth of *E. austin-smithii* is densely pubescent with coppery, simple, and dibrachiate hairs; the vestiture of *E. darcyi* is much sparser. The older branches of *E. darcyi* have large knobby nodes and gray, exfoliating bark; in *E. austin-smithii* the bark is brown and smooth, the nodes barely enlarged. The inflorescences of *E. austin-smithii* may be fasciculate, but are commonly short-racemose, the rachis 2–3 mm long, with flowers twice the size of *E. darcyi*, with twice as many stamens (ca. 100). The fruits of *E. darcyi* are obovoid or ellipsoid, with a thin pericarp, ca. 1 mm thick; *E. austin-smithii*'s are ovoid to broadly ellipsoid and fleshier, the pericarp 3–5 mm thick.

This species is named in honor of William G. D'Arcy. Of Bill's many notable accomplishments, not the least was taking charge of the *Flora of Panama*, a project that had been running for more than 40 years, and guiding it quickly and surely to a successful conclusion.

Paratypes. PANAMA. **Coclé:** above El Cope & Barrigon, near Continental Divide, 8°38'N, 80°35'W, 850 m, *McPherson 12165* (F, MO). **Panamá:** Cerro Jefe, *L. Carrasquilla 2191* (MO); Cerro Jefe near summit, beyond Goofy Lake, *M. D. Correa A. 710* (MO); alrededores de Cerro Jefe, 1007 m, *M. D. Correa et. al. 4567* (MO); Cerro Jefe, 750–900 m, *W. G. D'Arcy 12334* (MO); Cerro Jefe, beside radio tower, 900 m, *W. G. D'Arcy et al. 15504* (F, MO); Cerro Jefe, *J. A. Duke 9388* (MICH, MO); summit of Cerro Jefe, *J. D. Dwyer et al. 1029* (F, MO); Cerro Jefe, 850 m, *J. D. Dwyer et al. 7192* (MO), *J. D. Dwyer et al. 7292* (MICH); top of Cerro Jefe near antenna, 2 km below antenna, ca. 1000 m, *J. P. Folsom et al. 5657* (MO); región de Cerro Jefe, 9°14'N, 79°22'30"W, ca. 1000 m, *C. Galdames et al. 1609* (PMA); near top of Cerro Jefe to 1 mi. beyond, *A. Gentry & J. Dwyer 3535* (MO); E slope of Cerro Jefe, 1 m S of radio tower, 9°15'N, 79°30'W, 1000 m, *S. Knapp 3547* (MO); summit of Cerro Jefe, along road on E slope, 9°15'N, 79°30'W, 900–1000 m, *S. Knapp & M. Huft 4583* (MO); Cerro Jefe (or Cerro Azul), near radio tower, 9°15'N, 79°30'W, 950 m, *G. McPherson 7113* (MO); Cerro Jefe, along trail on ridge running NE from summit, ca. 1000 m, *S. Mori & J. Kallunki 3605* (MO); Cerro Jefe, 4 mi. past Cerro Azul on road to Altos Pacora, 850 m, *K. Sytsma & W. G. D'Arcy 3658* (F, MO).

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DEUX ESPECES NOUVELLES ET UNE COMBINAISON NOUVELLE CHEZ LES RUTACEAE DE L'ARCHIPEL DES COMORES

Jean-Noël Labat, Marc Pignal, and Olivier Pascal

Résumé. L'étude des caractères morphologiques permet la description de deux espèces nouvelles de Rutaceae de l'Archipel des Comores: *Ivodea choungiensis* Labat, M. Pignal & O. Pascal et *Vepris darcyi* Labat, M. Pignal & O. Pascal. Les récoltes récentes qui complètent la connaissance du taxon, amènent à la combinaison nouvelle, *Vepris unifoliolata* (Baill.) Labat, M. Pignal & O. Pascal.

Mots clés: Archipel des Comores, *Ivodea*, Mayotte, Rutaceae, *Vepris*.

Abstract. Morphological characters support the description of two new species of Rutaceae from the Comoro Archipelago: *Ivodea choungiensis* Labat, M. Pignal & O. Pascal and *Vepris darcyi* Labat, M. Pignal & O. Pascal. Recent collections, which add to our understanding of the taxon, allow us to make the following new combination: *Vepris unifoliolata* (Baill.) Labat, M. Pignal & O. Pascal.

Key words: Comoro Archipelago, *Ivodea*, Mayotte, Rutaceae, *Vepris*.

Les inventaires floristiques récents des plantes indigènes ou naturalisées de Mayotte menés par le Service de l'Environnement et de la Forêt de Mayotte en collaboration avec le Muséum national d'Histoire naturelle de Paris ont permis d'approfondir la connaissance de cette flore insulaire. Les récoltes systématiques réalisées lors de ce projet ont notablement enrichi les collections herbariologiques peu abondantes et souvent anciennes (voir en particulier Lowry et al., 1999). L'étude de ce nouveau matériel et la révision des spécimens de l'Archipel des Comores présents dans l'herbier du Muséum (P) nous ont amené à identifier plusieurs taxons nouveaux pour la science: une espèce de *Labramia* (Sapotaceae) (Labat et al., 1997), une de *Noronhia* et deux de *Chionanthus* (Oleaceae) (Labat et al., 1999), une de *Scolopia* et une d'*Erythrospermum* (Flacourtiaceae) (Hul et al., 1999), deux de *Cynometra* (Fabaceae–Caesalpinioideae) (Labat & Pascal, 1999), une de *Polyscias* (Araliaceae) (Lowry et al., 1999), une de *Nesogordonia* (Sterculiaceae) (Labat et al., 2001), une de *Drypetes* (Euphorbiaceae) (McPherson, 2000) et une de *Psiadia* (Asteraceae) (Labat & Beentje, 2004). D'autres nouveaux taxa seront publiés dans les prochaines années. Les explorations botaniques récentes et la publication de ces espèces nouvelles démontrent qu'un travail d'inventaire de la biodiversité est encore nécessaire dans cette petite île de l'Océan Indien. Sachant que la végétation naturelle de Mayotte ne couvre que moins de 5% de la superficie de l'île, il faut considérer que ces espèces, ainsi que tous les taxons endémiques de cette zone, sont fortement menacées et mériteraient des mesures de protection *in situ* et *ex situ* (Pascal, 2002 et Pascal et al., 2001).

La famille des Rutaceae n'était connue aux Comores que par trois genres: *Vepris* A. Juss., avec deux espèces endémiques (*V. parvicalyx* H. Perrier et *V. spathulata* (Engl.) H. Perrier), *Toddalia* Juss. (*T. asiatica* (L.) Lam.) et *Teclea* Del., avec deux espèces endémiques (*T. boiviniana* (Baill.) H. Perrier et *T. unifoliolata* Baill.) (Perrier de la Bâthie, 1950). Mziray (1992), lors de sa révision taxonomique de *Toddalieae* Hook.f., a considérablement fait évoluer la conception générique à l'intérieur de cette tribu. Seuls trois genres sont conservés, en particulier *Vepris* qui inclue huit genres, dont *Teclea*, auparavant considérés comme distincts. Cet auteur a publié une combinaison nouvelle pour une espèce comorienne, *V. boiviniana* (H. Perrier) W. Mziray, mais a considéré l'espèce *Teclea unifoliolata* comme un taxon insuffisamment connu. Le genre *Vepris* compte environ 80 espèces, il est présent en Afrique tropicale, à Madagascar, aux Mascareignes (avec *V. lanceolata* (Lam.) G. Don qui pousse également en Afrique (Coode, 1979, et Kokwaro, 1982)), ainsi qu'en Arabie et dans le sud-ouest de l'Inde. Le genre *Ivodea* Capuron (Capuron, 1961, 1967), qui comptaient 10 espèces endémiques de Madagascar, est signalé ici pour la première fois dans l'archipel des Comores auquel appartient l'île de Mayotte.

Ivodea choungiensis Labat, M. Pignal & O. Pascal, sp. nov. TYPE: Mayotte, Mlima Choungi, 12°57'20"S, 45°07'55"E, 450 m, 1er déc. 2000 (fl ♂), *J.-N. Labat & F. Barthelat 3343* (holotype, P00203087; isotypes G, K, *MAYOTTE*[1], MO, P00203086, P00203085, alcool: P00203084). Figure 1.

A. *I. trichocarpa* R. Cap., coriacioribus et adaxiale nitidis foliis, glabris petiolis, masculis glabris minoribus haud pyramidalisque inflorescentiis, sine lateralibus cristis masculis alabestris, praecipue differt.

Arbre de 10 m de hauteur et 30 cm de diamètre ou arbuste de 1,5 à 2 m, très ramifié. Rameaux à croissance définie, terminés par une inflorescence, écorce grisâtre, fissurée longitudinalement, sans lenticelles, jeune rameau glabre,

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[1] *Note.* L'herbier cité «*MAYOTTE*» ne possède pas d'acronyme officiel, il s'agit de l'herbier du Service de l'Environnement et de la Forêt de Mayotte.

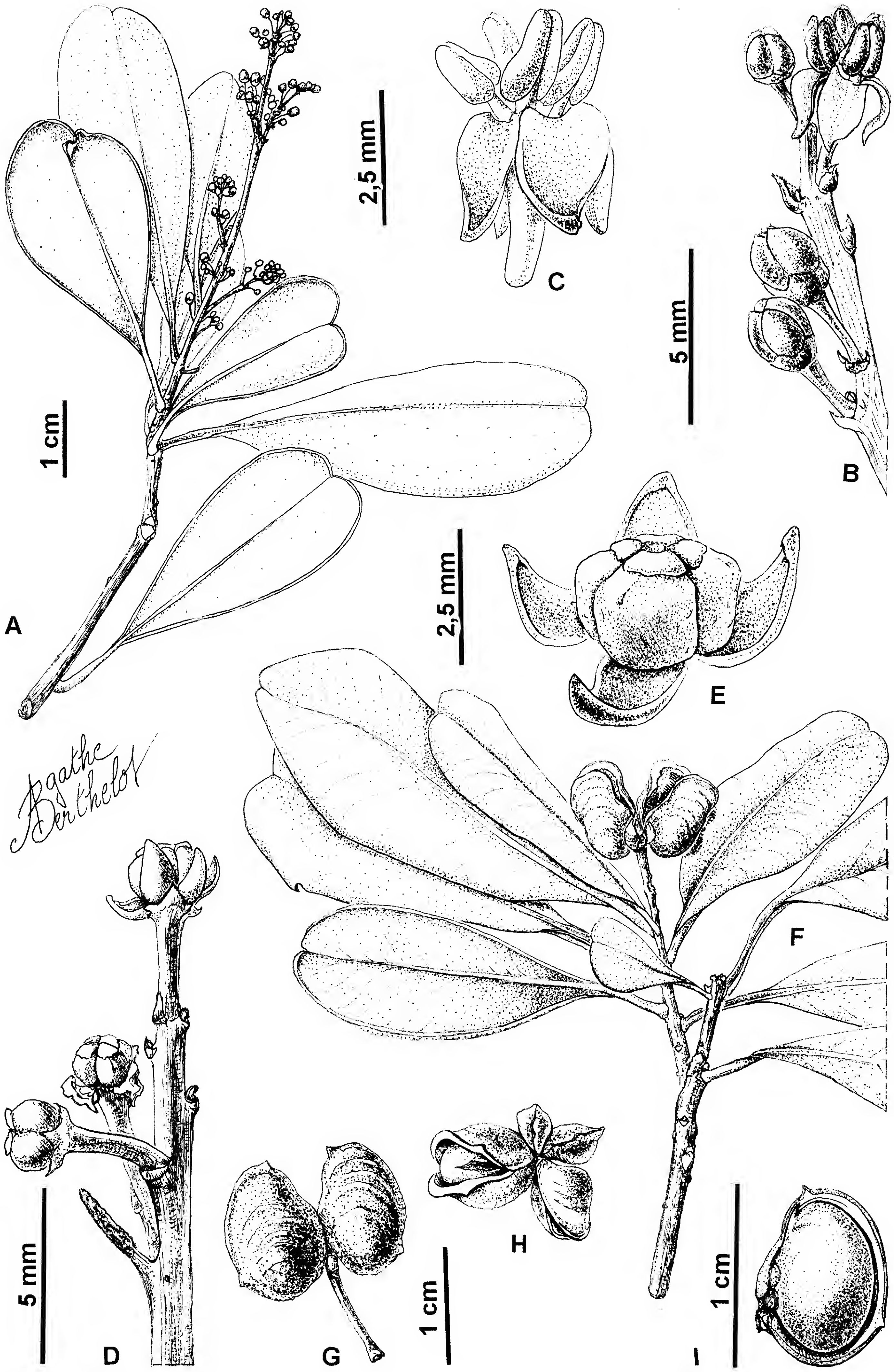
A
1 cm
2,5 mm
C
5 mm
B
2,5 mm
E
Agathe Barthelot
F
5 mm
D
G
1 cm
H
1 cm
I

Figure 1. *Ivodea choungiensis* Labat, M. Pignal & O. Pascal. —A. Rameau ♂, aspect général. —B. Portion d'inflorescence ♂. —C. Fleur ♂. —D. Portion d'inflorescence ♀. —E. Fleur ♀. —F. Rameau en fruit. —G, H. Fruits. —I. Fruit partiel ouvert et graine en place. (A, *O. Pascal 290;* B, C (type), *Labat & Barthelat 3343;* D, E & I, *Labat & Barthelat 3342;* F, *Pascal 212;* G, H, *Pignal, Pibot & Mas 1418.*)

cicatrices foliaires proéminentes. Feuilles simples, alternes, plutôt groupées ou sub-opposées à l'extrémité des rameaux. Pétiole long de 7–12 mm, glabre, épaissi aux deux extrémités, genouillé à l'extrémité terminale mais sans articulation visible, aplati à la face supérieure et légèrement ailé. Limbe sub-coriace, glabre, avec des ponctuations translucides bien visibles sur le frais, face supérieure vert luisant et inférieure plus mate, obové à oblong-elliptique, (3,4–)5–7,5 × 1,5–3,1 cm, sommet arrondi ou émarginé, base atténuée, marge récurvée; nervation brochidodrome légèrement saillante sur les deux faces de la même couleur que le reste du limbe (sur le matériel sec); 14 paires de nervures secondaires environ. Inflorescences ♂ terminales, allongées et étroites, d'environ 5 cm de longueur, sub-glabres, paniculiformes, à groupes de cymes de 1–10 fleurs, plus ou moins contractées, à l'aisselle de bractées triangulaires de 0,5 mm de longueur, caduques, ciliées au moins à l'apex (cils de 0,1 mm environ). Une paire de bractéoles ciliées linéaires à la base de chaque fleur. Fleur ♂ blanche. Bouton floral sphérique, avec 4 petites protubérances terminales. Calice cupuliforme, à 4 lobes peu marqués, triangulaires, arrondis, 0,6 × 0,4 mm, glabre, mais extrémité des pointes ciliée. Corolle à préfloraison valvaire, à 4 pétales lancéolés de 1,5 × 1 mm, terminés par un épaississement bien visible sur le bouton. Etamines 4, de 1,5 mm de hauteur, anthère 0,7 mm, à fentes longitudinales. Gynécée rudimentaire, 0,5 mm environ, à poils blancs. Inflorescence ♀ longue de 2 cm, terminale, pauciflore, à groupes de cymes à l'aisselle d'une bractée caduque de 3 × 0,5 mm. Fleurs ♀ à l'extrémité d'axes pouvant atteindre 2 mm, portant une ou deux paires de bractéoles de 0,8 × 2 mm, sub-opposées, triangulaires, ciliées et à poils épars. Pédicelle de 4 mm. Sépales 4–5, verts à lobes triangulaires de 1,6 × 1 mm. Pétales blancs, 4–5, lancéolés, caducs, 1,2 × 2,4 mm. Gynécée à 4–5 carpelles libres, stigmate jaunâtre aplati, cordiforme. Staminodes absents. Infrutescence terminale de 1,5–3 cm de longueur, portant 2 à 6 fruits. Fruit constitué de 2–5 fruits partiels dont trois sont souvent avortés, d'environ 1,3 × 0,8 cm, en forme de coquille d'huître et à ornementations en ondulations concentriques assez marquées; valves s'ouvrant sur les 2/3 de la longueur, base de chaque fruit partiel anguleuse. Pédicelle de 5–8 mm. Graine 9 × 6 mm, sans albumen, 2 cotylédons dont un replié; embryon de 1,2 mm.

Répartition et écologie. L'espèce n'est connue qu'à Mayotte, dans la forêt humide résiduelle du Mont Choungi. Il est à noter que cette répartition en population très isolées est également observée chez la plupart des espèces d'*Ivodea* à Madagascar (Capuron, 1967).

Phénologie. Floraison connue en mai, septembre et décembre, fructification en novembre et mai–juin.

Noms vernaculaires. Mvory voa, Sary honko (en shibuchi).

Statut de conservation. Avec une zone d'occupation estimée à moins de 10 km^2 et n'existant que dans un seul site dont la zone d'occupation et la qualité de l'habitat est en déclin suite aux aménagements du sommet du Mont Choungi, *Ivodea choungiensis* peut être considérée comme gravement menacée d'extinction (CR B1 + 2c) selon les critères de l'IUCN (1994).

Note. Les graines sans albumen permettent de rapporter sans ambiguïté le matériel étudié au genre *Ivodea* R. Cap. La présence ou l'absence de staminodes chez la fleur femelle, ainsi que le degré de soudure des styles, sont des caractères importants pour distinguer des taxons à l'intérieur de ce genre (Capuron, 1961). L'espèce morphologiquement la plus proche est *I. trichocarpa* R. Cap., mais *I. choungiensis* en diffère par ses feuilles coriaces et luisantes à la face supérieure au lieu de chartacées et glauques, ses pétioles glabres au lieu de pubescents, ses inflorescences ♂ glabres plutôt que pileuses, courtes (5 cm de longueur) et étroites plutôt que longues (jusqu'à 10 cm de longueur) et pyramidales, ses boutons floraux ♂ sphériques avec 4 petites protubérances terminales au lieu d'être munis de 4 petites ailes. Les staminodes sont absents, alors que chez *I. trichocarpa*, seul un cycle alternipétale de pièces très réduites est présent. Le style et le stigmate sont plus développés et cordiformes.

Etymologie. En raison de son endémisme local, cette espèce prend le nom du mont Choungi.

Paratypes. MAYOTTE. Grande Terre, Chirongi, Mont Choungi, Réserve Forestière, 18 nov. 2002 (fr), ***F. Barthelat, P. Hoffman, H. Ralimanana, M. M'Changama & A.B. Sifary 1085*** (*MAYOTTE*, P); Mlima Choungi, 12°57'20"S, 45°07'55"E, 450 m, 1er déc. 2000 (fl ♀ & fr), ***J.-N. Labat & F. Barthelat 3342*** (*MAYOTTE*, P); Choungi, 2 mai 1999 (fr), ***C. Mas 129*** (P); Mlima Choungi, 16 nov. 1995 (fr), ***O. Pascal 212*** (G, K, *MAYOTTE*, MO, P); Mlima Choungi, 29 déc. 1995 (fl ♂), ***O. Pascal 290*** (*MAYOTTE*, P); Mlima Choungi, 580 m., 17 juin 1996 (fr), ***O. Pascal 595*** (K, *MAYOTTE*, P); Mont Choungi, 12°57'20"S, 45°07'55"E, 2 mai 1999 (fl ♂), ***M. Pignal, A. Pibot & C. Mas 1413*** (G, P); Mlima Choungi, zone arbustive à proximité du sommet, 12°57'20"S, 45°07'55"E, 2 mai 1999 (fr), ***M. Pignal, A. Pibot & C. Mas 1418*** (P); Mlima Choungi 21 sep. 2001, face opposée au GR (fl ♀, fr), ***M. Pignal, F. Barthelat, M. M'Changama & A.B. Sifary 1921*** (B, G, K, MA, *MAYOTTE*, P).

Vepris darcyi Labat, M. Pignal & O. Pascal, sp. nov. TYPE. Mayotte, Bénara, 450 m, 05 mars 1996 (fl ♂), *O. Pascal 402* (holotype, P00179952; isotypes, K, *MAYOTTE*, MO, P00179953). Figure 2.

A *V. elliotii* (Radlk.) Verdoorn papyraceis ellipticis cuspidatisque majoribus foliolis, brevioribus inflorescentiis, distincte lobato calyce, elongatis staminibus praecipue differt.

Arbre dioïque de 7 à 10 m, à feuilles alternes. Feuilles unifoliolées. Pétiole long de 6–15 mm, glabre, canaliculé, légèrement renflé aux deux extrémités. Foliole elliptique, (6–)9–14 × (2,3–)3,5–5,5 cm, glabre, sub-sessile, point d'attachement de la foliole légèrement genouillé, base cunée, extrémité à cuspide de 10–15 mm de longueur et d'env. 4 mm de largeur en son centre, terminée par un apex arrondi. Limbe papyracé, vert clair sur le matériel sec, à marge très légèrement récurvée, ponctuations denses, visibles par transparence. Nervure primaire très saillante au dessous, peu saillante au dessus, 12–16 paires de nervures secondaires, fines, peu visibles. Inflorescences ♂ axillaires ou subterminales, panicules, rarement divisées en deux dès la base, portant 1 à 3 fascicules de 3 à 7 fleurs sur des bourrelets, glabres, sessiles ou faiblement pédonculés, pédoncule jusqu'à 5 mm de longueur, panicule plus court ou aussi long que le pétiole, pédicelles des fleurs grêles, long de 4–5 mm à maturité, bractées très petites de 0,1 mm environ. Fleur ♂ 4-mère, crème, de 4–5 mm de diamètre. Calice cupuliforme, de 0,5 mm de hauteur et 1,5 mm de diamètre, à 4 lobes triangulaires terminés par une petite pointe, portant sur la face extérieure 4 glandes allongées. Corolle à 4 pétales, libres, triangulaires, 2 × 1,5 mm, alternes par rapport aux lobes du calice. Etamines, 8, à filet filiforme de 0,8–1,2 × 0,1 mm. Anthères 1 × 0,5 mm, introrses, basifixes, déhiscentes par deux fentes latérales. Ovaire rudimentaire, pyramidal, de 1 mm de haut à 4 loges, 4 ébauches de style. Inflorescences ♀ similaires aux inflorescences ♂ mais réduites à 3–5 fleurs. Fleur ♀ 4-mère, crème, 6 mm de diamètre. Calice identique à celui de la fleur ♂. Corolle à 4 pétales libres, ovés-lancéolés, légèrement inégaux de 2,8–3 × 1–1,5 mm, épais, pourvus d'un ergot à l'extrémité de la face intérieure. Staminodes présents, 8, caducs très tôt, appliqués contre l'ovaire, anthère longue de 0,3 mm. Ovaire globuleux de 2 mm de diamètre, glabre, à 4 loges à paroi épaisse, 2 ovules par loge, 4 stigmates grossièrement cordiformes, soudés, sessiles, noirs, formant un disque tétralobé à bords récurvés. [Fruit inconnu.]

Répartition et écologie. Espèce peu fréquente des dernières forêts humides de l'île. Elle est cependant mieux représentée dans la forêt relique à tendance mésophile du plateau de Sohoa sur la côte ouest. Cette forêt, située à 200 m d'altitude, présente un cortège d'espèces particulier qui la distingue des forêts plus humides des massifs du Bénara ou du M'Tsapéré au centre et au nord-est de l'île (Pascal et al., 2001).

Phénologie. Floraison connue en mars, avril et septembre.

Noms vernaculaires. Sary hompi malandi, Sary tsoha (en shibushi).

Statut de conservation. Avec une zone d'occupation estimée à moins de 10 km^2 dangereusement fragmentée et un déclin constaté de la

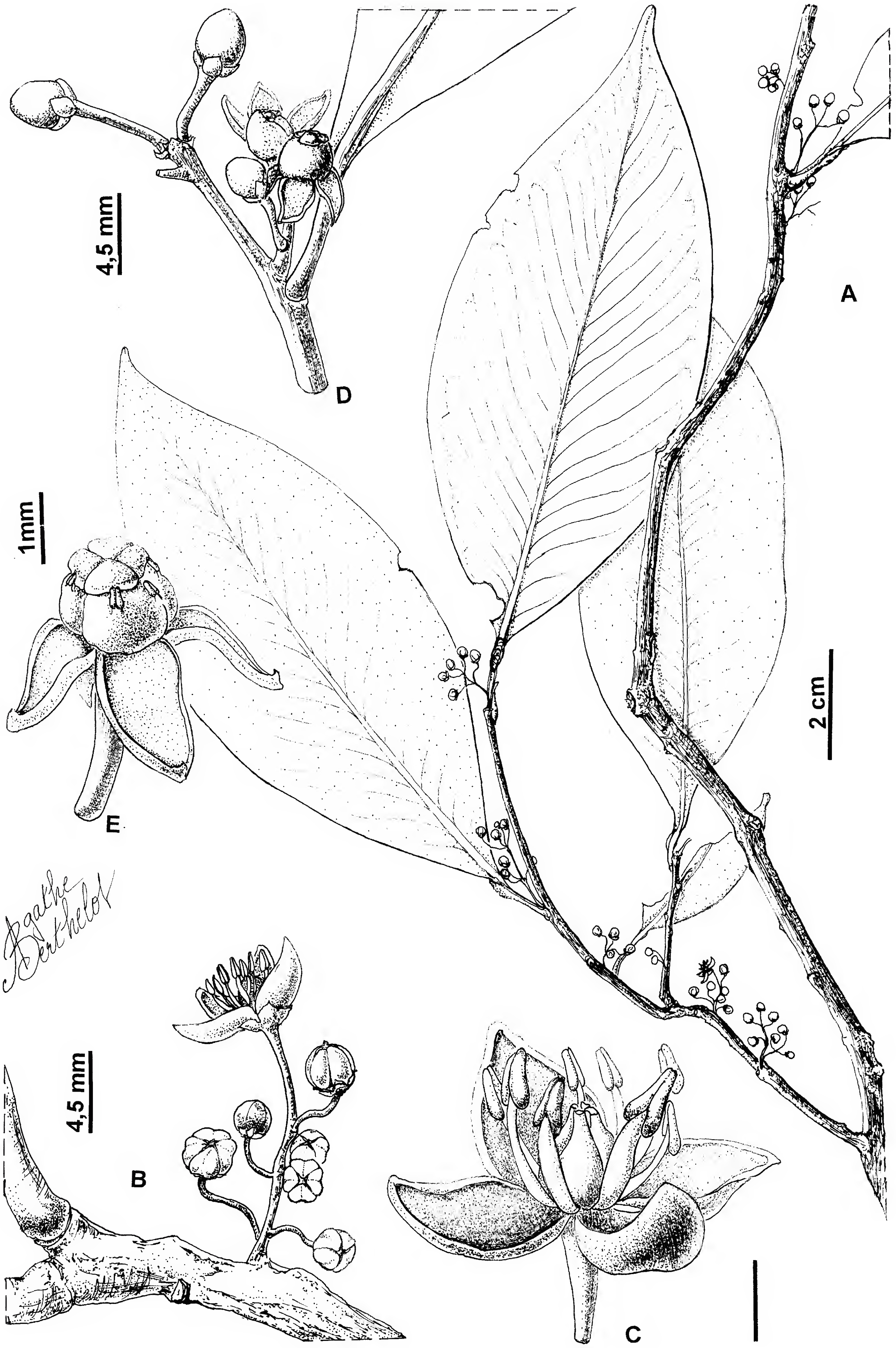
A
B
C
D
E
4,5 mm
1mm
2 cm
4,5 mm
Agathe Berthelot

Figure 2. *Vepris darcyi* Labat, M. Pignal & O. Pascal. —A. Rameau ♂, aspect général. —B. Inflorescence ♂. —C. Fleur ♂. —D. Inflorescence ♀. —E. Fleur ♀. (A–C, *Pascal 456;* D, E, *Pascal 455.*)

zone d'occupation et de la qualité de l'habitat constitué par les forêts humides de Mayotte, *Vepris darcyi* peut être considérée comme gravement menacée d'extinction (CR B1 + 2c) selon les critères de l'IUCN (1994).

Note. Vepris darcyi appartient à la section I définie par Perrier de la Bâthie (1948, 1950), caractérisée par un gynécée rudimentaire formé de 4 carpelles stériles dans les fleurs mâles et un ovaire à 4 loges dans les fleurs femelles. Parmi les espèces à feuilles unifoliolées de cette section, *V. darcyi* est proche d'un groupe à ovaire glabre et à gynécée rudimentaire de la fleur mâle pyramidal (*V. nitida* Verdoorn, *V. madagascarica* (Baill.) H. Perrier, *V. elliotii* (Radlk.) Verdoorn et *V. sclerophylla* H. Perrier). La structure des inflorescences assez réduite en panicules axillaires ou subterminales rapproche *V. darcyi* de *V. elliotii* et de *V. madagascarica*. Contrairement à *V. darcyi*, *V. madagascarica* possède une fleur mâle dépourvue de staminodes. *Vepris darcyi* diffère de *V. elliotii* par la texture, la forme et la taille de ses folioles, papyracées, elliptiques et cuspidées au lieu de rigides, oblancéolées ou oblongues-obovales et obtuses au sommet, de (6–)9–14 × (2,3–)3,5–5,5 cm contre 3–7 × 1,2–2,2 cm, par ses inflorescences plus courtes ne dépassant pas la longueur du pétiole au lieu d'atteindre au moins la moitié de la longueur du limbe, son calice à 4 lobes triangulaires terminés par une petite pointe et non obscurément lobulé, à lobes arrondis. *Vepris spathulata* (Engl.) H. Perrier, décrite de Mayotte et retrouvée lors des inventaires récents, appartient également à la section I des *Vepris* de Perrier de la Bâthie, mais diffère clairement de *V. darcyi* par ses feuilles étroitement oblongues, ses inflorescences cauliflores et son calice à limbe réduit à un étroit rebord à peine sinueux. *Vepris parvicalyx* H. Perrier n'est connue que d'Anjouan et de la Grande Comore où elle semble plus abondante. Egalement de la section I des *Vepris* de Perrier de la Bâthie, cette dernière diffère de *V. darcyi* par ses feuilles plus coriaces, ses inflorescences terminales amples et pyramidales, ses pédicelles floraux trapus et son calice dont le limbe est réduit à un étroit rebord à peine sinueux.

Etymologie. Cette espèce est dédiée à William Gerald D'Arcy en reconnaissance de son travail sur la flore de Madagascar et des Comores.

Paratypes. MAYOTTE. Grande Terre, Chiconi, réserve forestière de Sohoa, 5 avr. 2001 (fl ♂), F. Barthelat, B. Simmen, L. Tarnaud, J. Fred, M. M'Changama & A.B. Sifary 345 (G, K, *MAYOTTE*, MO, P); Grande Terre, Chiconi, réserve forestière de Sohoa, 4 sept. 2001 (fl ♂), F. Barthelat, M. Pignal, M. M'Changama & A.B. Sifary 481 (B, G, K, *MAYOTTE*, MO, P); Sohoa, 200 m, 2 avril 1996 (fl ♀), ***O. Pascal 455*** (P, *MAYOTTE*); Sohoa, 200 m, 2 avril 1996 (fl ♂), ***O. Pascal 456*** (P, *MAYOTTE*).

Vepris unifoliolata (Baill.) Labat, M. Pignal & O. Pascal, comb. nov. Basionyme: *Teclea unifoliolata* Baill., Bull. Mens. Soc. Linn. Paris 1: 591. 1886. TYPE: Mayotte, forêt de Combani, 20 oct. 1884 (fl ♂), *L. Humblot 1364* (lectotype, choisi ici, P00198156; isolectotype P00198157).

Comoroa pisocarpa Oliv., Hooker, Icon. Pl. t. 2048. 1895. TYPE: Grande Comore, *Kirk s.n.* (K non vu).

Mziray (1992) considère *Teclea unifoliolata* comme un taxon insuffisamment connu du genre *Vepris*, et ne fait donc pas la combinaison nouvelle de cette espèce. En fait, il cite par erreur comme type *Kirk s.n.*, en effet cette récolte est en réalité le type de *Comoroa pisocarpa* et non de *T. unifoliolata*. La diagnose originale de *T. unifoliolata* (Baillon, 1886: 592) signalait plusieurs spécimens, dont l'un, « *Boivin*, Nossibé, ad. riv. Andradroite » a été rapproché par Perrier de la Bâthie (1948, 1950) de *Teclea punctata* Verdoorn (plus précisément d'une variété non validement publiée car sans diagnose latine). Ce rapprochement reste incertain étant donné que ce spécimen est stérile et qu'il s'agit de feuilles (anormalement grandes) d'un jeune pied. Les autres syntypes, dont le lectotype choisi ici, correspondent bien au même taxon qui était ainsi parfaitement connu (fleurs des deux sexes et fruits présents parmi les syntypes), d'autant plus qu'il a été souvent récolté depuis sur les quatre îles de l'archipel (voir la liste du matériel étudié dans la base de données SONNERAT sur le site <http://www.mnhn.fr/base/sonnerat.html>).

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21

SIX NEW *GAERTNERA* (RUBIACEAE) SPECIES FROM MADAGASCAR AND PHYLOGENETIC ANALYSES THAT SUPPORT *HYMENOCNEMIS* AS A SYNONYM OF *GAERTNERA*

Simon T. Malcomber and Aaron P. Davis

ABSTRACT. The phylogenetic status of *Hymenocnemis* relative to *Gaertnera* (Rubiaceae) is examined for the first time using nucleotide sequence data from non-coding regions of the nrDNA internal transcribed spacer region (ITS) and two copies of phosphoenolcarboxylase (*PepC*) genes. Our phylogenetic analysis indicates that *Hymenocnemis madagascariensis* and three of six new species with usually one-flowered inflorescences, connate stipules, secondarily superior ovaries, and glabrous corolla lobes are nested within a well-supported *Gaertnera* clade. Of the seven characters originally used to diagnose *Hymenocnemis*, two characters occur throughout the tribe Gaertnereae (*Gaertnera* and *Pagamea*) and five are widespread among *Gaertnera* species. We conclude that the molecular and morphological data do not support the acceptance of *Hymenocnemis*, and the continued recognition of *Hymenocnemis* as a separate genus would make *Gaertnera* paraphyletic. In this paper we formally make the new combinations *G. madagascariensis* (Hook. f.) S. T. Malcomber & A. P. Davis and *G. furcellata* (Baill. ex Vatke) S. T. Malcomber & A. P. Davis, and describe six new *Gaertnera* species: *G. alata* Bremek. ex S. T. Malcomber & A. P. Davis, *G. bambusifolia* S. T. Malcomber & A. P. Davis, *G. brevipedicellata* S. T. Malcomber & A. P. Davis, *G. darcyana* S. T. Malcomber & A. P. Davis, *G. microphylla* Capuron ex S. T. Malcomber & A. P. Davis, and *G. pauciflora* S. T. Malcomber & A. P. Davis. Distribution maps are provided for all species and four species are illustrated. A key to all *Gaertnera* species with one- or few-flowered inflorescences is provided. Conservation assessments are given for all the species treated herein, using the criteria set by the IUCN.

Key words: conservation, Gaertnereae, internal transcribed spacer (ITS), Madagascar, nrDNA, phosphoenolcarboxylase (*PepC*).

The phylogenetic relationship between the Rubiaceae genera *Hymenocnemis* Hook. f. and *Gaertnera* Lam. is currently unknown. *Hymenocnemis* is a monotypic Malagasy genus containing the single species *H. madagascariensis* Hook. f. It was first described on the basis of connate stipules, which cap the young growing tip; solitary, axillary, 4-merous flowers with unequal-sized calyx lobes; anthers with apical appendages and a bilocular ovary (Hooker, 1873). *Gaertnera*, in contrast, is a morphologically diverse, paleotropical genus of approximately 70 species with a distribution encompassing the humid evergreen forests of West and Central Africa, Madagascar, the Mascarenes, Sri Lanka, and Southeast Asia (Malcomber, 2002). Counter to expectations based on the widespread distribution and morphological disparity among *Gaertnera* species, molecular phylogenetic studies suggest that the genus has radiated recently and rapidly, probably within the last 5.5 million years (Malcomber, 2002). *Gaertnera* and its South American sister genus *Pagamea* together constitute the well-supported tribe Gaertnereae, which is diagnosed by the presence of a secondarily superior ovary, sheathing stipules, xylem with parenchyma bands, and compound pollen apertures with crescent-shaped costae (Igersheim et al., 1994; Jansen et al., 1996b; Bremer & Manen, 2000; Malcomber, 2002). *Gaertnera* differs morphologically from *Pagamea* in the presence of glabrous corolla lobes (Malcomber, 2002).

The superior ovary typical of *Gaertnera* and *Pagamea* species led to alternative placements for the genera within the Loganiaceae and Rubiaceae. *Gaertnera*, first described by Lamarck (1792), was considered the type of a new family intermediate between the Rubiaceae and Apocynaceae by Jussieu (1807). Brown (1814) included *Gaertnera* and *Pagamea* in his new family Loganeae (or Loganiaceae) along with *Geniostoma*, *Logania*, *Usteria*, and, doubtfully, *Fagraea*. Van Martius (1827), De Candolle (1845), and Bentham and Hooker (1876) all classified the two genera within the Loganiaceae based on the presence of superior ovaries. Baillon (1879) first proposed that *Gaertnera* and *Pagamea* belonged within the Rubiaceae. He noted that the superior ovary was partially fused at the base and not completely free as in other Loganiaceae. This placement was later supported by Solereder (1891), who reported the presence of raphides and the absence of intra-xylary phloem in the two genera, characters otherwise unknown within Loganiaceae, but widespread within Rubiaceae. Recent molecular, palynological, and anatomical analyses have all confirmed the placement of *Gaertnera* and *Pagamea* within the Rubiaceae and suggest a close relationship between these genera and the Psychotrieae and Morindeae (Andersson & Rova, 1999; Bremer, 1996; Bremer & Manen, 2000; Jansen et al., 1996a, 1996b, 1997; Nepokroeff et al., 1999).

When Hooker (1873) described *Hymenocnemis*, only flowering material was available. The ovary in *H. madgascariensis*, as in *Gaertnera* (see Igersheim et al., 1994), is semi-inferior in the flower and only becomes superior secondarily during fruit development. Baker (1884) was the first to hypothesize a close relationship between *Gaertnera* and *Hymenocnemis*. Later, Capuron (unpublished ms.) went as far as to consider *Hymenocnemis* a synonym of *Gaertnera* based on the shared presence of fused stipules and a secondarily superior ovary, but never made the combination for *H. madgascariensis.*

Hymenocnemis is allied to *Gaertnera* based on the presence of fused stipules, a secondarily superior ovary, and glabrous corolla lobes, but the phylogenetic relationship between these genera has never been explicitly examined and the taxonomic combination has not been made. In the course of broader monographic and evolutionary studies, seven Malagasy species have been discovered with connate stipules, secondarily superior ovaries, glabrous corolla lobes, and usually one-flowered inflorescences. One of these species is currently placed within *Psychotria* (*P. furcellata* Baill. ex Vatke). C. E. B.

Bremekamp associated this taxon with *Hymenocnemis*, but never made the combination for *H. furcellata*. The remaining six species are new. The discovery of these taxa has underscored the necessity of resolving the phylogenetic relationship between *Hymenocnemis* and *Gaertnera* to ensure that these species are either associated with, or described within, the correct genus.

In this paper we report the results of a phylogenetic analysis of *Gaertnera*, *Hymenocnemis*, and closely related Rubiaceae genera using nucleotide sequence data from the three noncoding nDNA regions: the nrDNA internal transcribed spacer (ITS) and two copies of the fourth intron of the low copy nDNA phosphoenolpyruvate carboxylase (*PepC*) gene (*PepC*-Large and *PepC*-Small). On the basis of our analysis, which is supported by morphological data, we conclude that *Hymenocnemis* is nested within *Gaertnera* and should not be recognized as a separate genus. *Hymenocnemis madagascariensis* is transferred to *Gaertnera*, as is *Psychotria furcellata* Baill. ex Vatke. The aforementioned six new species are further described within *Gaertnera*. In the remainder of this paper we will refer to *Hymenocnemis madagascariensis* Hook. f. as *Gaertnera madagascariensis*, *Psychotria furcellata* as *Gaertnera furcellata*, and the six new species as *Gaertnera alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darcyana*, *G. microphylla*, and *G. pauciflora*, to reflect our new taxonomy.

MATERIALS AND METHODS

MORPHOLOGY

The seven morphological characters used by Hooker (1873) to diagnose *Hymenocnemis* were examined in 68 *Gaertnera* species, *Morinda citrifolia* L., *M. royoc* L., and *Pagamea guianensis* Aubl. These characters are connate stipules (character 1), stipules that cap the young growing tip (character 2), solitary, axillary flowers (character 3), 4-merous flowers (character 4), flowers with unequal-sized calyx lobes (character 5), anthers with apical appendages (character 6), and bi-locular ovary (character 7). Herbarium specimens and/or spirit collections were examined from A, BM, BR, BRUN, CGE, E, FHO, GH, G, G-DC, K, KEP, L, MAU, MO, P, PDA, SAN, SAR, SING, TAN, TEF, UBD, W, WAG, and WU.

MOLECULAR PHYLOGENETICS

ITS, *PepC*-Large (*PepC*-L), and *PepC*-Small (*PepC*-S) sequences for 24 *Gaertnera* species, *Pagamea guianensis*, and the outgroups *Morinda citrifolia* and *Morinda royoc*, as used by Malcomber (2002), were supplemented with ITS sequences for *G. microphylla* and *G. humblotii*. In addition, ITS, *PepC*-L, and *PepC*-S sequences were generated for *G. longevaginalis* (Table 1). The 27 *Gaertnera* species included in this study span the entire geographical range of the genus (Gabon, Democratic Republic of Congo, Madagascar, Mauritius, Sri Lanka, Malaysia, and Brunei Darussalam) and include three of the new species and one of the new combinations included in this paper (Table 1). Leaf material of the remaining four species treated herein (*G. alata*, *G. bambusifolia*, *G. darcyana*, and *G. furcellata*) was either unavailable or did not yield DNA of sufficient quality for successful PCR amplification.

Total genomic DNA was extracted from silica-dried leaves using the CTAB miniprep protocol of Doyle and Doyle (1987). Double-stranded PCR products of the ITS region were amplified using the primers ITSLEU1 and ITS4, and the two copies of the fourth intron of *PepC* were amplified using the primers PEPCX4F and PEPCX5R in 50 µl PCR reactions as described in Malcomber (2002). The ITS PCR reactions produced a single product of approximately 650 bp, whereas the *G. longevaginalis PepC* PCR reactions amplified two distinct products of approximately 450 bp and 900 bp. PCR products were gel purified using Qiaquick columns (Qiagen Inc., Valencia, California) and subcloned using pGEM-T easy vector systems (Promega Corp., Madison, Wisconsin). Plasmid DNA was cleaned using an alkaline lysis/PEG precipitation protocol (Sambrook et al., 1989) prior to sequencing. ITS clones were sequenced

TABLE 1. Taxa included within the phylogenetic analysis.[1] = Sequences used in Malcomber (2002).

Taxon	Tribe	Voucher information	GenBank accession number		
			ITS	PepC-L	PepC-S
Gaertnera brevipedicellata S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, *Malcomber 2876* (MO, TEF)	AF333819[1]	AY046373[1]	AY046345[1]
Gaertnera cooperi Hutch. & M. B. Moss	Gaertnereae	Gabon, *Jongkind 4982* (MO)	AF333820[1]	AF333851[1]	AF333879[1]
Gaertnera cuneifolia Bojer	Gaertnereae	Mauritius, *Malcomber 2940* (MAU, MO)	AF333821[1]	AY046376[1]	AY046347[1]
Gaertnera drakeana A. DC.	Gaertnereae	Madagascar, *Malcomber 2802* (MO, TEF)	AF333822[1]	AF333853[1]	AY046349[1]
Gaertnera edentata Bojer	Gaertnereae	Mauritius, *Malcomber 2961* (MO, MAU)	AF333823[1]	AF333854[1]	AF333882[1]
Gaertnera fractiflexa Beusekom	Gaertnereae	Malaysia, *Malcomber 3033* (MO, SAR)	AF333824[1]	AF333855[1]	AY046357[1]
Gaertnera globigera Beusekom	Gaertnereae	Malaysia, *Malcomber 3038* (MO, SAR)	AF333825[1]	AF333856[1]	AY046333[1]
Gaertnera hispida Aug. DC.	Gaertnereae	Madagascar, *Malcomber 2824* (MO, TEF)	AF333826[1]	AF333857[1]	AF333885[1]
Gaertnera humblotii E. Drake	Gaertnereae	Madagascar, *McPherson 17623* (MO)	AF360696	—	—
Gaertnera inflexa Baill.	Gaertnereae	Madagascar, *Malcomber 2886* (MO, TEF)	AF333827[1]	AF333858[1]	AY046336[1]
Gaertnera junghuhniana Miq.	Gaertnereae	Brunei Darussalam, *Malcomber 2965* (MO, BRUN)	AY046326[1]	AY046377[1]	AY046365[1]
Gaertnera longevaginalis (Schweinf. ex Hiern) E. M. A. Petit	Gaertnereae	Democratic Republic of Congo, *Harris 3176* (MO)	AY185549	AY185550	AY185551
Gaertnera longifolia Bojer	Gaertnereae	Mauritius, *Malcomber 2935* (MAU, MO)	AF333829[1]	AF333860[1]	AY046337[1]
Gaertnera macrostipula Baker	Gaertnereae	Madagascar, *Malcomber 2774* (MO, TEF)	AF333831[1]	AF333862[1]	AY046343[1]

Gaertnera madagascariensis (Hook. f.) S. T. Malcomber & A. P. Davis new comb. [=*Hymenocnemis madagascariensis* Hook. f.]	Gaertnereae	Madagascar, *Malcomber 2865* (MO, TEF)	AF333832[1]	AF333863[1]	AF333891[1]
Gaertnera microphylla S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, *Malcomber 2925* (MO, TEF)	AF360697	—	—
Gaertnera oblanceolata King & Gamble	Gaertnereae	Malaysia, *Malcomber 3039* (MO, SAR)	AF333836[1]	AF333867[1]	AF333895[1]
Gaertnera paniculata Benth.	Gaertnereae	Democratic Republic of Congo, *Harder 3751* (MO)	AY046329[1]	AF333864[1]	AF333892[1]
Gaertnera pauciflora S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, *Malcomber 2772* (MO, TEF)	AF333834[1]	AF333865[1]	AF333893[1]
Gaertnera psychotrioides Baker	Gaertnereae	Mauritius, *Malcomber 2946* (MO, MAU)	AF333835[1]	AF333866[1]	AY046362[1]
Gaertnera ramosa Ridl.	Gaertnereae	Malaysia, *Malcomber 3012* (KEP, MO)	AF333816[1]	AF333847[1]	AY046338[1]
Gaertnera rosea Thwaites ex Benth.	Gaertnereae	Sri Lanka, *Malcomber 2758* (MO, PDA)	AF333837[1]	—	AF333896[1]
Gaertnera schizocalyx Bremek.	Gaertnereae	Malaysia, *Malcomber 3036* (MO, SAR)	AF333839[1]	AF333869[1]	AY046355[1]
Gaertnera ternifolia Thwaites	Gaertnereae	Sri Lanka, *Malcomber 2766* (MO, PDA)	AY046331[1]	AF333870[1]	AY046361[1]
Gaertnera vaginans (DC.) Merr.	Gaertnereae	Sri Lanka, *Malcomber 2763* (MO, PDA)	AF333841[1]	—	AY046350[1]
Gaertnera viminea Hook. f. ex C. B. Clarke	Gaertnereae	Singapore, *Malcomber 3010* (MO, SING)	AF333842[1]	AF333871[1]	AY046354[1]
Gaertnera walkeri (Arn.) Blume	Gaertnereae	Sri Lanka, *Malcomber 2764* (MO, PDA)	AF333843[1]	AF333872[1]	AY046356[1]
Morinda citrifolia L.	Morindeae	Unknown origin, Cultivated, Pacific Tropical Botanical Garden, *Wood 960867*	AF333844[1]	AF333873[1]	AF333903[1]
Morinda royoc L.	Morindeae	Unknown origin, Cultivated, Pacific Tropical Botanical Garden, *Wood 880320*	AF333845[1]	AF333874[1]	AY046370[1]
Pagamea guianensis Aubl.	Gaertnereae	Guyana, *Taylor 12079* (MO)	AF333846[1]	—	AF333905[1]

using plasmid primers T7 and SP6 and internal primers ITS2 (White et al., 1990) and ITS3B (Baum et al., 1994). To check for intra-individual variation among ITS paralogs, two to four clones were sequenced and dimethysulfoxide was used in both the PCR and sequencing reactions, following the recommendations of Buckler et al. (1997). *PepC* clones were sequenced in both directions using plasmid primers T7 and SP6 for the 450 bp *PepC*-S product and primers T7, PEPCINTF, PEPCINTR, and SP6 for the 900 bp *PepC*-L product as described in Malcomber (2002). Dideoxy sequencing was conducted using the BigDye dye terminator cycle sequencing protocol (from Applied Biosystems, Foster City, California) and sequencing reactions were analyzed on an ABI377 (Applied Biosystems) automated DNA sequencer.

Preliminary alignment of the ITS, *PepC*-L, and *PepC*-S sequences was performed using Clustal W (Thompson et al., 1994), before being manually edited using MacClade 4.0 (Maddison & Maddison, 2003). Sequences were analyzed using a combination of maximum parsimony (MP) and maximum likelihood (ML) methods implemented in PAUP* 4.0 (Swofford, 2000). MP searches used the heuristic search option with TBR and MULPARS and 100 random addition sequence replicates. MP bootstrap support (Felsenstein, 1985) was estimated based on 1000 bootstrap replicates using the heuristic search option with TBR, MULPARS, random addition, and MAXTREES set to 5000. Only branches supported by > 50% bootstrap values are indicated in the strict consensus tree (Fig. 1), but only branches > 70% bootstrap are considered well supported (Hillis & Bull, 1993). Optimal parameters for the ML search were estimated using PAUP* 4 and Modeltest 3.06 (Posada & Crandall, 1998). ML searches used the heuristic search option with TBR and MULPARS and 10 random sequence additions.

TAXONOMIC TREATMENT

Descriptions of the two new combinations (*Gaertnera madagascariensis* and *G. furcellata*) and six new species (*G. alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darcyana*, *G. microphylla*, and *G. pauciflora*) were based on 62 collections from K, MO, P, TAN, and TEF, plus 11 collections made in the course of this research that will be distributed to A, BR, G, K, LE, MAL, MAU, P, PRE, TEF, UPS, and/or WAG. Geo-referenced specimens were analyzed spatially using Geographic Information Systems (GIS) and assigned to vegetation type and underlying geology using the base map developed by Du Puy and Moat (1996). The conservation status of each species was assigned using GIS in combination with the IUCN Red Data Book Criteria (IUCN, 2001).

RESULTS

MORPHOLOGY

Of the seven characters used by Hooker (1873), connate stipules (character 1) are found in all *Gaertnera* species and are considered synapomorphies for the Gaertnereae (Jansen et al., 1996b; Bremer & Manen, 2000; Malcomber, 2002). Similarly, bi-locular ovaries (character 7) are found in all Gaertnereae, in addition to many species of Psychotrieae and Morindeae (Robbrecht, 1988), including *Morinda citrifolia* and *M. royoc*. Stipules similar to *G. madagascariensis*, which cap the growing tip (character 2), are also found in 21 additional African, Malagasy, and Mascarene *Gaertnera* species, including *G. cooperi*, *G. cuneifolia*, *G. drakeana*, *G. hispida*, and *G. longifolia*, in addition to *G. alata*, *G. brevipedicellata*, *G. furcellata*, *G. microphylla*, and *G. pauciflora*. Although originally described by Hooker (1873) as only having an axillary inflorescence, our survey of *G. madagascariensis* specimens indicated that the inflorescences are always terminal, although they can be terminal on short side branches or terminal-overtopped (initiated in a terminal position but overtopped by the growing shoot: as in many *Psychotria* spp.). The inflorescences are never axillary. The inflorescences are usually 1-flowered, although sometimes 3- or 4-flowered inflorescences are observed. *Gaertnera* species usually have between 9 and more than 100 flowers per inflorescence. Solitary (or occasionally 3/4) flowered inflorescences (character 3) are uncommon within the genus, but can also be found in the Sri Lankan species *G. ternifolia*, in addition to *G. furcellata* and all of the new species described herein (*G. alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darcyana*, *G. microphylla*, and *G. pauciflora*). Flower merosity (character 4) is variable within *G. madagascariensis*, as in most other *Gaertnera* species, with individual plants frequently having both 4- and 5-merous flowers, including the new species *G. brevipedicellata* and *G. pauciflora*. However, consistently 4-merous flowers occur in 10 Malagasy, Sri Lankan, and Southeast Asian species, including *G. fractiflexa*, *G. inflexa*, *G. rosea*, and *G. viminea*, the new combination *G. furcellata*, and the new species *G. alata* and *G. microphylla*. Unequal calyx lobes (character 5) are found in 10 African and Malagasy *Gaertnera* species, including *G. humblotii* and the new species *G. darcyana*. Different sized calyx lobes are most pronounced in the Malagasy species *G. phyllostachya* and *G. phyllosepala*, where the larger lobe may reach 15 mm long and is expanded into a petaloid calycophyll. Anthers with slight terminal extensions are found in *Gaertnera* species throughout the distributional range of the genus. However, anthers with prominent apical appendages (character 6), similar to those seen in *G. madagascariensis*, are relatively uncommon; they occur in at least six additional Malagasy, Mascarene, and Sri Lankan *Gaertnera* species including *G. edentata*, *G. rosea*, and the new species *G. pauciflora*. The distribution of these seven characters is mapped onto the phylogeny that is discussed below (Fig. 1).

MOLECULAR PHYLOGENETICS

The *Gaertnera humblotii*, *G. longevaginalis*, and *G. microphylla* ITS sequences ranged from 622 to 625 bp, and no intra-individual variation was detected among the ITS paralogs. The *G. longevaginalis PepC*-L sequence was 896 bp and the *PepC*-S sequence 452 bp. The aligned matrix of 2049 bp yielded 238 (11.6%) phylogenetically informative characters. The MP and ML searches recovered very similar topologies (Fig. 1). The equally weighted parsimony analysis, with gaps treated as missing data, resulted in 1980 equally most parsimonious trees of 363 steps with CI = 0.793, RI = 0.811 (uninformative characters removed). The best-fitting likelihood model was the General Time Reversal (GTR—Lanave et al., 1984), with gamma-distributed rates (i.e., GTR + G). The ML search recovered a single topology with a likelihood score of -ln 6463.42 that was identical to one of the equally most-parsimonious trees (Fig. 1).

In the MP and ML phylogenetic trees the *Gaertnera* clade is well supported (100% MP bootstrap) and is subtended by a branch 18 unambiguous characters long in the MP analysis. Because of the limited sequence divergence among *Gaertnera* species, likely due to the recent and rapid radiation of the genus (Malcomber, 2002), few relationships within the *Gaertnera* clade are supported by > 70% MP bootstrap. *Gaertnera madagascariensis* (= *Hymenocnemis madagasacariensis*) and the three new species (*G. brevipedicellata*, *G. microphylla*, and *G. pauciflora*) are nested within a Malagasy *Gaertnera* clade. *Gaertnera madagascariensis* and *G. microphylla* form a well-supported clade (79% MP bootstrap) that is nested within a clade containing *G. drakeana*, *G. hispida*, *G. humblotii*, *G. macrostipula*, and the new species *G. pauciflora*. Aside from the *G. madagascariensis* and *G. microphylla* clade, none of the relationships estimated by the ML analysis within this clade are supported by > 50% MP bootstrap and all collapse in the MP strict consensus (Fig. 1). The other new species, *G. brevipedicellata*, forms a clade with the Malagasy *G. inflexa* in both the MP strict consensus and ML trees, but this relationship is not supported by MP bootstrap > 50% (Fig. 1).

CONCLUSIONS

A review of the seven characters used by Hooker (1873) to diagnose *Hymenocnemis* indicates that two of the characters (bi-locular ovary and connate stipules) are found in all *Pagamea* and *Gaertnera* species, one of the characters (4-merous flowers) is variable within *G. madagascariensis*, and the remaining four characters (stipules that cap the growing tip, usually one-flowered inflorescences, unequal calyx lobes, and anthers with prominent apical appendages) are widespread among *Gaertnera* species. The phylogenetic analysis of the ITS, *PepC*-L, and *PepC*-S nucleotide sequence data indicates that *G. madagascariensis* (= *Hymenocnemis madagascariensis*) and three of the new species are nested within a well-supported *Gaertnera* clade. These results indicate that the continued acceptance of *Hymenocnemis* will make *Gaertnera* paraphyletic. Although the three remaining new species (*G. alata*, *G. bambusifolia*, and *G. darcyana*) and combination (*G. furcellata*) were not included within the molecular analysis, all possess the connate stipules, secondarily superior ovaries, and glabrous corolla lobes that diagnose *Gaertnera* species.

In summary, the phylogenetic analysis and survey of morphological characters used to diagnose *Hymenocnemis* both support Capuron's conclusion that *Hymenocnemis* should be regarded as a synonym of *Gaertnera* (Capuron, unpublished ms.). The transfer of *Hymenocnemis madagascariensis* and *Psychotria furcellata* to *Gaertnera*, and description of the six new *Gaertnera* species with usually 1(but occasionally 3 or 4)-flowered inflorescences are made below.

TAXONOMIC TREATMENT

A key to the 1(to 3 or 4)-flowered species in Madagascar and Sri Lanka is given below. Only the Malagasy species are subsequently treated, as the Sri Lankan species have been described previously and will be treated in another contribution (Malcomber, in prep.).

KEY TO 1–3- OR 4-FLOWERED *GAERTNERA* SPECIES IN MADAGASCAR AND SRI LANKA

1a. Young stipules exclusively calyptrate, typically caducous or occasionally apex marcescent, membranous or chartaceous; Madagascar.

  2a. Stem internodes not ridged.

    3a. Young branchlets and stipules distinctly pubescent; calyx lobes narrowly triangular to linear, 0.5–4 mm long.....6. *G. madagascariensis* comb. nov.

    3b. Young branchlets and stipules usually glabrous but rarely pubescent; calyx lobes triangular, 0.1–0.4 mm long.....8. *G. pauciflora* sp. nov.

  2b. Stem internodes distinctly ridged.

    4a. Stipules caducous, longitudinal ridge present when young; corolla pale pink or pink.

      5a. Pedicels 2.5–19 mm long; corolla 7.5–11.5 mm long..... 1. *G. alata* sp. nov.

      5b. Pedicels ± absent; corolla 3–3.5 mm long................ 3. *G. brevipedicellata* sp. nov.

    4b. Stipules persisting as 4 membranous remnants, longitudinal ridge absent; corolla white.

      6a. Leaves elliptic, apex acuminate (or very briefly cuspidate)... 5. *G. furcellata* comb. nov.

      6b. Leaves obovate to spathulate, apex mucronulate... 7. *G. microphylla* sp. nov.

1b. Young stipules calyptrate or cylindrical, cylindrical or funnel-shaped when older, apex persistent, chartaceous or coriaceous, rarely membranous; Madagascar and Sri Lanka.

  7a. Stem internodes not ridged; Madagascar.

    8a. Leaves linear-lanceolate to lanceolate; pedicels 9–30 mm long, calyx lobes absent or triangular and up to 0.4 mm long...2. *G. bambusifolia* sp. nov.

8b. Leaves linear-lanceolate to elliptic; pedicels 2–6 mm long; calyx lobes prominent, triangular to linear, 0.4–3.1 mm long... 4. *G. darcyana* sp. nov.

7b. Stem internodes ridged; Sri Lanka.

9a. Leaves opposite, sometimes ternate, linear-lanceolate or elliptic, tertiary venation distinct; corolla salverform.............*G. ×gardneri*

9b. Leaves always ternate, linear-oblong, tertiary venation indistinct; corolla campanulate... *G. ternifolia*

Note (*): Not included in this treatment.

Gaertnera Lam., Tabl. Encycl. Meth., Bot. t. 167. 13 Feb. 1792; 2: 273. 31 Oct. 1819 (nom. cons.), non *Gaertnera* Schreber (1789), non *Gaertnera* Retz (1791), non *Gaertneria* Medik. (1789), non *Gaertneria* Necker (1790). *Andersonia* Willd. ex Roem. & Schult. (1819), non *Andersonia* R. Brown (1810). TYPE: *Gaertnera vaginata* Poir.

Fructesca DC. ex Meisn., Pl. Vasc. Gen. 1: 259; 2: 168. 1840. TYPE: *Fructesca mauritiana* DC. ex Meisn.

Hymenocnemis Hook. f., in Bentham & Hooker f., Gen. 2: 132. 1873. TYPE: *Hymenocnemis madagascariensis* Hook. f.

Pristidia Thwaites, Enum. Pl. Zeyl. 2: 149. 1859. TYPE: *Pristidia divaricata* Thwaites.

Sykesia Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 351. 1836. TYPE: *Sykesia koenigii* Arn., nom. illeg. (*Psychotria vaginans* DC., *S. vaginans* (DC.) O. Kuntze (Rev. Gen. 2: 426. 1891)) (*vide* Pfeiffer, Nom. 2: 1325. 1874).

1. **Gaertnera alata** Bremek. ex S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antananarivo: Forêt d'Andasibe, bassin de l'Onive, 19°50´S, 47°51´E, Feb. 1925, *H. Perrier de la Bâthie 17098* (holotype, P!).

Haec species *Gaertnerae madagascariensi* similis, sed ab ea ramulis glabris alatisque, foliis ellipticis vel elliptico-oblongis, stipulis juvenilibus ala angusta per tubi medium percurrente ornatis atque floribus pallide roseis vel roseis distinguitur.

Shrub 1–2 m tall; *branchlets* terete, 0.5–3 mm diam., usually ± 2-winged, ± corky, pale beige to gray or whitish, glabrous; internodes with 2 or 3 longitudinal ribs, 0.3–2.7 cm long. *Leaves* paired, elliptic to elliptic-oblong, or ± elliptic-obovate, 0.6–3.6 × 0.3–1.8 cm, chartaceous, glabrous; base cuneate to rounded; apex acute to abruptly acuminate; secondary veins distinct on the underside of the leaf blade, 3 to 5(to 8) pairs on each side of the costa; domatia present, in axils between costa and secondary veins, distinctly pubescent; petioles 0.9–3 mm long, not furrowed; *stipules* marcescent or sometimes caducous, adnate and tubular for most of their length, calyptrate, membranous, pubescent or puberulous; tube 2–6.6 mm long, with ribs forming distinct narrow wings beneath the petiole and 2 ribs, 1 each side, vertically down the middle of the stipule tube; apex (free part) with 2 opposite incisions, marcescent, 2-lobed, lobes 0.7–1.2 mm long, deltate. *Inflorescence* terminal and/or terminal on axillary branches, 1- to 3(or 4)-flowered, if more than 1-flowered ± cymose, lacking axes, sessile (peduncle absent), erect, lax; bracteoles absent; pedicels 2.5–19 mm long, glabrous or puberulous. *Flowers* 4-merous, *long-styled flowers*: unknown; *short-styled flowers*: calyx cup-shaped to ± urceolate, 1.5–2.6 mm wide, glabrous, hair-ring (inside calyx) indistinct; lobes triangular to narrowly triangular to linear, 0.4–4 mm long; corolla clavate in bud, salverform when open, 7.5–11.5 × 4.2–12 mm, pale pink to pink, outside and inside glabrous; lobes 2.6–6.1 mm long, triangular to narrowly triangular, apex acute, inside glabrous; anthers included, filaments inserted just below the middle of tube, ca. 0.5 mm long; style 2.7–5.4 mm long, glabrous, stigma ca. 0.8 mm long; *short-styled flowers*: unknown. *Drupes* unknown.

Distribution and ecology. Madagascar, known only from escarpment forest south of Tsinjoarivo, southeast of Ampatolampy in evergreen humid forest, 1400 to 1550 m, on metamorphic and igneous basement rocks (Fig. 2). Recorded growing on rocks.

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN** B1ab(i,ii,iii) +2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 5000 km^2 (for *G. alata*: EOO not possible to calculate as based on two data points but certainly less than 5000 km^2); a—known to exist in no more than five locations (for *G. alata*: three collections giving two geo-reference points, representing two locations); b (i–iii)—continuing decline projected due to inferred degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km^2 (for *G. alata*: 4.4 km^2 based on two cells of 1.48 km^2); B2ab—as for B1. On the basis of EOO and AOO, *G. alata* qualifies for the Critically Endangered Category (CR). However, the number of collections is greater than one (a CR criterion) and satellite imagery (J. Moat, pers. comm.) shows that this species occurs in good quality, relatively unbroken, escarpment forest (i.e., unlikely to be severely fragmented).

Phenology. Flowering in January and February; fruiting time unknown.

Gaertnera alata is distinct from the other few-flowered *Gaertnera* species by a combination of its 2-winged, more or less corky branchlets (similar to some variants of *G. microphylla*); pubescent domatia; calyptrate, marcescent, pubescent stipules, with a prominent longitudinal ridge when young; long pedicels (2.5–19 mm long); and large (7.5–11 mm long) pale pink to pink flowers.

This species was provisionally named by C. E. B. Bremekamp on a specimen held at the Paris herbarium (*H. Perrier de la Bâthie 17098*, P)—with the annotation: "*Hymenocnemis alata* Brem. n. spec. C. E. B. Bremekamp VI 1951"—but this name was never published by him. We take the opportunity here to name this distinct species as *Gaertnera alata*.

Paratypes. MADAGASCAR. **Antananarivo:** 16.2 km SE de Tsinjoarivo, le long de la rivière d'Andrindrimbola, *N. Messmer & F. Andriatsiferana NM 690* (G, K), *N. Messmer & F. Andriatsiferana NM 692* (G, K).

2. Gaertnera bambusifolia S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antsiranana: Réserve Naturelle de Marojejy, along trail to the summit of Marojejy Est, NW of Mandena, wet, evergreen forest above the second camp, 14°26´S, 49°15´E, 850–1000 m, 11 Feb. 1989, *J. Miller & P. Lowry 3978* (holotype, MO!; isotypes, K!, P!, TAN!).

Haec species *Gaertnerae madagascariensi* similis, sed ab ea planta omnino glabra, foliis anguste lanceolatis, stipulis cylindricis subpersistentibus atque pedicellis longioribus 9–30 mm longis distinguitur.

Tree, ca. 3 m tall; *branchlets* terete, 0.5–2 mm diam., glabrous; internodes not ribbed, 0.8–4 cm long. *Leaves* paired; linear-lanceolate to lanceolate, 2.5–7 × 0.5–1.5 cm, chartaceous, glabrous; base cuneate to obtuse; apex cuspidate; secondary veins distinct on the underside of the leaf blade, 4 to 6 pairs on each side of the costa; domatia absent; petioles 1.3–4.5 mm long, not furrowed; *stipules* caducous, cylindrical, membranous, glabrous; tube 4.5–5.5 mm long, stipular ribs indistinct; apex entire, marcescent, 4-lobed, lobes filiform, 0.3–0.5 mm long. *Inflorescence* terminal and/or terminal on axillary branchlets, 1-flowered, pendent; bracteoles inserted on the pedicel or at base of calyx, indistinct; pedicel 9–30 mm long, glabrous. *Flowers* 5-merous; calyx cup-shaped, 1.9–2.5 mm wide, glabrous, hair-ring (inside calyx) absent; lobes absent, or triangular and up to 0.4 mm long; corolla clavate in bud, mature corolla unknown. *Drupes* subglobose or bilobed, 5.5—6 × 5—6 mm, smooth, green (immature), glabrous; (1 or) 2 pyrenes per drupe, mature pyrenes unknown.

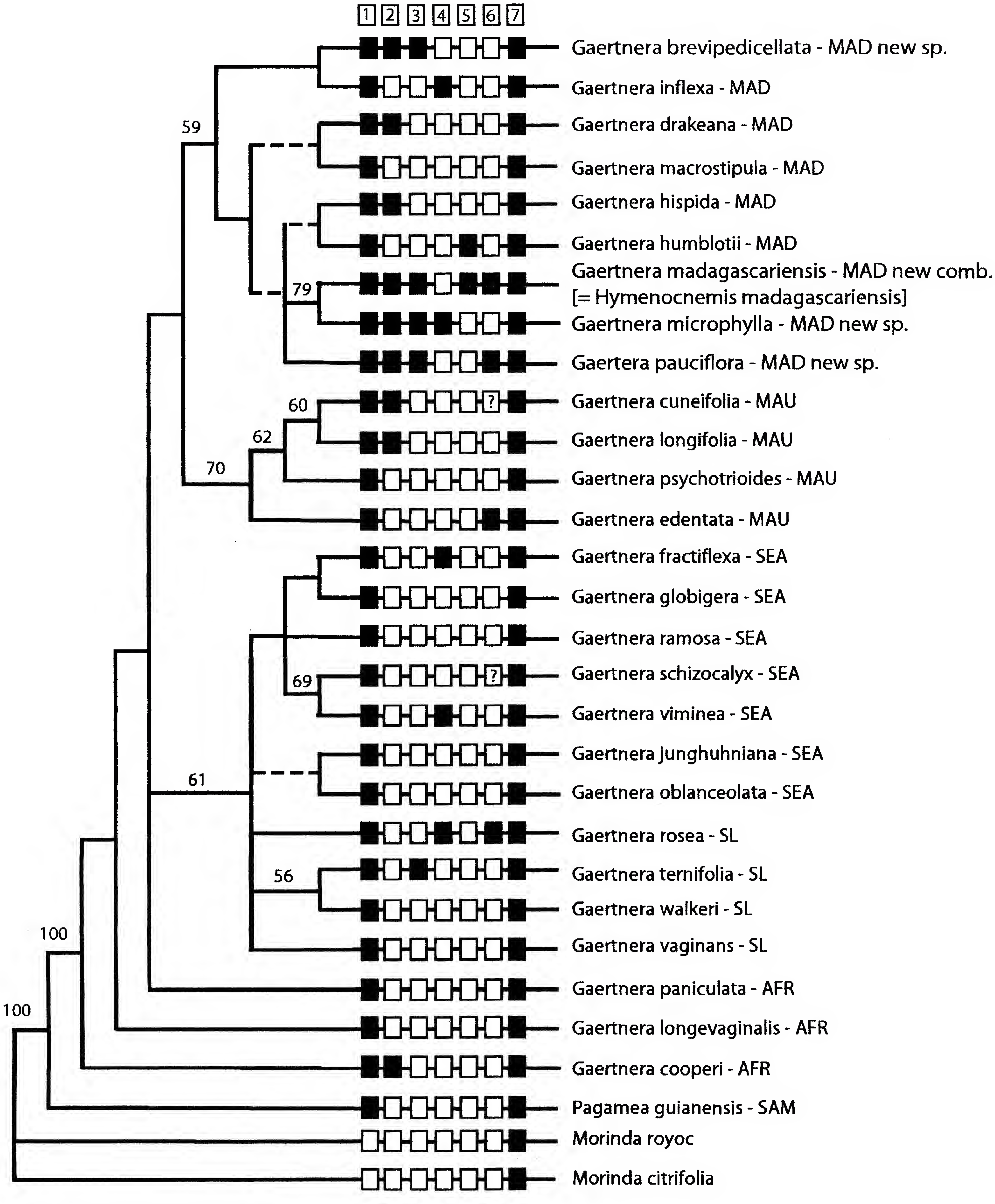
1
2
3
4
5
6
7
Gaertnera brevipedicellata - MAD new sp.
Gaertnera inflexa - MAD
Gaertnera drakeana - MAD
Gaertnera macrostipula - MAD
Gaertnera hispida - MAD
Gaertnera humblotii - MAD
Gaertnera madagascariensis - MAD new comb.
[= Hymenocnemis madagascariensis]
Gaertnera microphylla - MAD new sp.
Gaertera pauciflora - MAD new sp.
Gaertnera cuneifolia - MAU
Gaertnera longifolia - MAU
Gaertnera psychotrioides - MAU
Gaertnera edentata - MAU
Gaertnera fractiflexa - SEA
Gaertnera globigera - SEA
Gaertnera ramosa - SEA
Gaertnera schizocalyx - SEA
Gaertnera viminea - SEA
Gaertnera junghuhniana - SEA
Gaertnera oblanceolata - SEA
Gaertnera rosea - SL
Gaertnera ternifolia - SL
Gaertnera walkeri - SL
Gaertnera vaginans - SL
Gaertnera paniculata - AFR
Gaertnera longevaginalis - AFR
Gaertnera cooperi - AFR
Pagamea guianensis - SAM
Morinda royoc
Morinda citrifolia
59
79
60
62
70
69
61
56
100
100
?
?

Figure 1. Maximum likelihood (ML) and maximum parsimony (MP) phylogenies of the combined ITS, *Pep*C-L, and *Pep*C-S data set of 27 *Gaertnera* species, *Morinda citrifolia, M. royoc,* and *Pagamea guianensis.* Dashed branches collapse in the MP strict consensus tree. MP bootstrap values > 50% indicated above the branches. Distribution of 7 characters (1–7) used by Hooker (1873) to diagnose *Hymenocnemis.* 1 = connate stipules; 2 = stipules that cap the young growing tip; 3 = 1(to 3)-flowered inflorescences; 4 = exclusively 4-merous flowers; 5 = flowers with unequal-sized calyx lobes; 6 = anthers with prominent apical appendages; 7 = bi-locular ovary. ?= unknown, ■ = present, □ = absent. AFR = Africa, MAD = Madagascar, MAU = Mauritius, new sp. = new species, new comb. = new combination, SAM = South America, SEA = Southeast Asia, SL = Sri Lanka.

Distribution and ecology. Madagascar, Marojejy National Park and Anjanaharibe-Sud Nature reserve. In evergreen, humid forest, from 850 to 1235 m, on metamorphic and igneous basement rocks or quartzite (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN** B1ab(i,ii,iii) +2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 5000 km^2 (for *G. bambusifolia*: EOO not possible to calculate as based on two data points but certainly less than 5000 km^2); a—known to exist in no more than five locations (for *G. bambusifolia*: two collections giving two geo-reference points, representing two locations); b (i–iii)—continuing decline projected due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km^2 (for *G. bambusifolia*: 16.3 km^2 based on two cells of 2.9 km^2); B2ab—as for B1.

Phenology. Flowering unknown; fruiting February–March.

Gaertnera bambusifolia is a poorly known species represented by two recent fruiting herbarium collections from protected areas in northeastern Madagascar. The species is named for its distinctive lanceolate leaves, which resemble bamboo leaves, and are unknown among other usually one-flowered *Gaertnera* species. *Gaertnera bambusifolia* differs from other *Gaertnera* species treated herein by the combination of lanceolate leaves, cylindrical stipules, and long, slender pedicels (9–30 mm long). *Gaertnera bambusifolia* and *G. pauciflora* co-occur in mid-altitude humid, evergreen forests in Marojejy National Park and might be confused due to both species having slender pedicels. However, the two species can be easily differentiated based on leaf shape (lanceolate in *G. bambusifolia* vs. elliptic to oblanceolate in *G. pauciflora*), stipules (cylindrical in *G. bambusifolia* vs. calyptrate in *G. pauciflora*), and pedicel length (9–30 mm in *G. bambusifolia* vs. 2.5–9.1 mm in *G. pauciflora*).

Paratype. MADAGASCAR. **Antsiranana:** Andapa, Ambodiangezoka, Ambodisatrana, Anjanaharibe-Sud Special Réserve, *D. Ravelonarivo 680* (K, MO, P, TAN).

3. Gaertnera brevipedicellata S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Fianarantsoa: Ranomafana National Park, Talatakely, 800–900 m, 21°16′S, 47°25′E, 5 Nov. 1997, *S. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2877* (holotype, MO!; isotypes, BR!, G!, K!, P!, PRE!, TEF!, WAG!). Figure 3.

Haec species *Gaertnerae madagascariensi* similis, sed ab ea stipulis glabris in mediano tubi porca longitudinali prominente munitis atque floribus sessilibus distinguitur.

Shrub, 2–6 m tall; *branchlets* terete, 0.5–3 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.4–4.5 cm long. *Leaves* paired, elliptic or ovate, 0.8–3.8 × 0.4–2 cm, chartaceous, glabrous; base cuneate or attenuate; apex acuminate; secondary veins distinct on the underside of the leaf blade, 3 to 5 pairs on each side of the costa; domatia absent; petioles 1.2–2.8 mm long, not furrowed; *stipules* caducous, calyptrate, membranous, glabrous; tube 1.6–7.5 mm long, with ribs forming distinct narrow wings beneath the petiole and 2 ribs, 1 each side, vertically down the middle of the stipule tube; apex (free part) with a single interpetiolar cleft or with 2 opposite incisions, marcescent, 4-lobed, lobes 0.4–1 mm long, linear. *Inflorescence* terminal on axillary branchlets, 1-flowered, erect; bracts leaf-like; bracteoles inserted on the pedicel or at base of calyx (or rarely absent) indistinct; pedicel ± absent. *Flowers* 4- or 5-merous, bisexual, heterodistylous; *long-styled flowers*: calyx cup-shaped, 1.5–3.5 mm wide, glabrous, hair-ring (inside calyx) absent; lobes narrowly triangular to linear, 1.1–4.2 mm long; corolla clavate in bud, salverform when open; 3–3.5 x 1.4–2.5 mm, pink, glabrous outside, inside with a ring of villous hairs in about the middle, lobes triangular or hemi-elliptic, 3.5–4.8 mm long, inside glabrous, apex acute; anthers included, filaments inserted in about the middle of tube, up to 0.2 mm long; style 4.5–5.5 mm long, glabrous, stigma

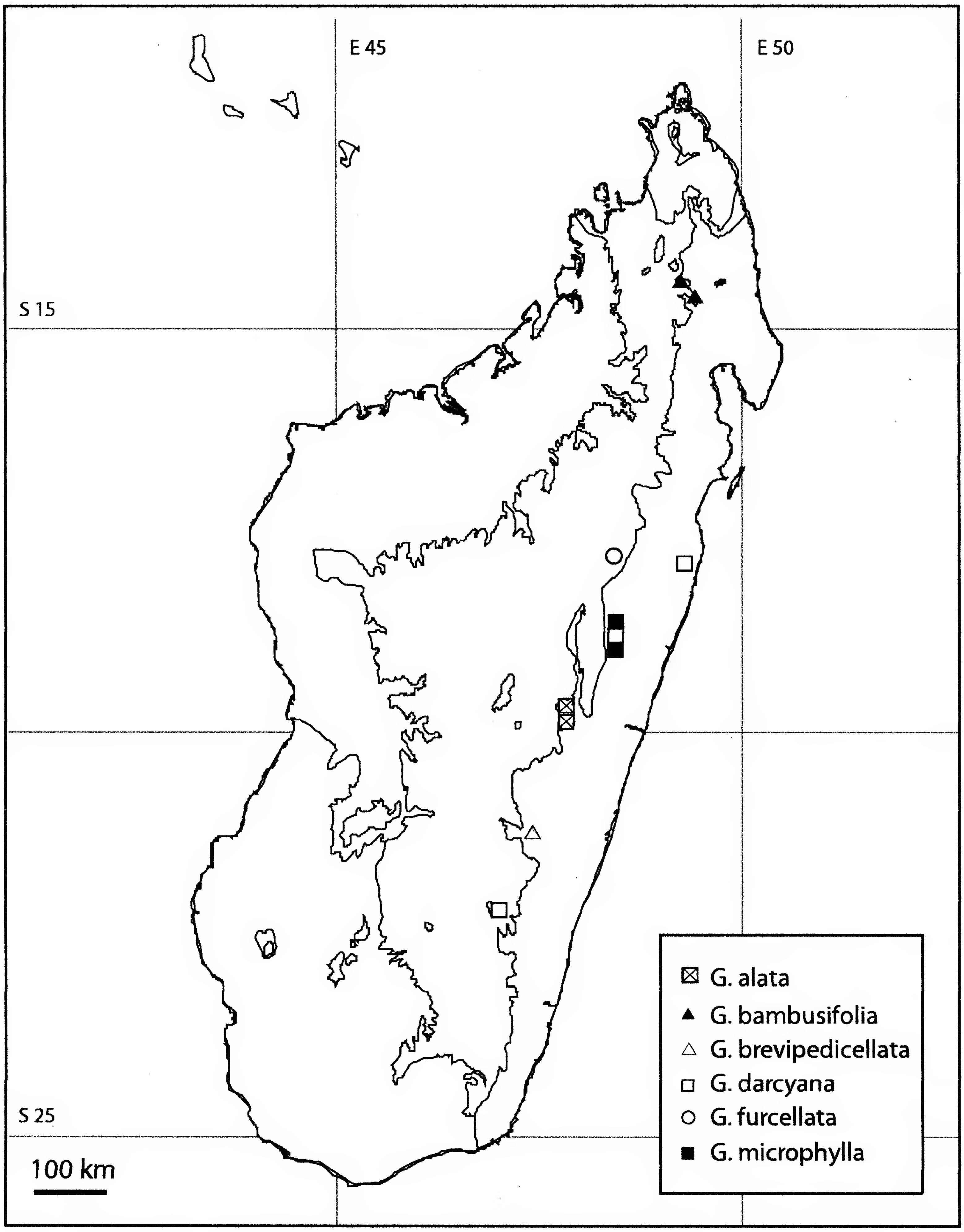
E 45
E 50
S 15
S 25
100 km
☒ G. alata
▲ G. bambusifolia
△ G. brevipedicellata
□ G. darcyana
○ G. furcellata
■ G. microphylla

Figure 2. Distribution of *Gaertnera alata, G. bambusifolia, G. brevipedicellata, G. darcyana, G. furcellata,* and *G. microphylla* mapped on the bioclimatic zones of Madagascar (after Cornet, 1974; see Schatz, 2000).

1–1.2 mm long; *short-styled flowers*: calyx cup-shaped, 1.5–2 mm wide, glabrous outside, hair-ring (inside calyx) absent; lobes narrowly triangular to linear, 1–4.5 mm long; corolla clavate in bud, salverform when open; 4–5.5 × 1–2.5 mm, pink, outside glabrous, inside with a ring of villous hairs in about the middle, lobes triangular to hemi-elliptic, 4–5 mm long, inside glabrous, apex acute; anthers just-exserted, filaments inserted in about the middle of tube, 2.5–3.5 mm long; style 1.5–2 mm long, glabrous, stigma 1.5–1.6 mm long. *Drupes* subglobose or bi-lobed, 4.5–5.5 × 4.5–7 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Ranomafana National Park. In evergreen humid forest, 800 to 1000 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN** B1ab(i,ii,iii) +2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 5000 km^2 (for *G. brevipedicellata*: 1.6 km^2); a—known to exist in no more than five locations (for *G. brevipedicellata*: four collections giving four geo-reference points, representing three locations); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km^2 (for *G. brevipedicellata*: 0.1 km^2 based on two cells of 0.18 km^2); B2ab—as for B1.

Phenology. Flowering in November; fruiting unknown.

Gaertnera brevipedicellata, named for its more or less sessile flowers, is diagnosed by a combination of glabrous vegetative and sexual parts, stem internodes and stipules with prominent longitudinal ridges, and pink, more or less sessile flowers. Despite a relatively high botanical collecting intensity in Ranomafana National Park within the past 20 years, the species is only known from three recent collections in the Talatakely and Vatoharanana regions, where the species is encountered only rarely. The paucity of *G. brevipedicellata* collections probably results from a combination of restricted distribution, local rarity, and inconspicuous flowers.

Paratypes. MADAGASCAR. **Fianarantsoa:** Ranomafana National Park, Talatakely, ***A. Kotozafy 1073*** (MO, TEF), ***S. Malcomber 2876*** (MO, TEF); Vatoharanana, ***S. Malcomber 2867*** (MO, TEF).

4. Gaertnera darcyana S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Toamasina: 11.9 km N of Andasibe, Mantadia National Park, 18°49′S, 48°26′E, 930 m, 21 Nov. 1997, *S. Malcomber, A. Davis, D. Gower & J. Andriantiana 2921* (holotype, MO!; isotypes, BR!, K!, P!, TEF!, WAG!).

Haec species *Gaertnerae obovatae* similis, sed ab ea stipulis cylindricis subpersistentibus, inflorescentia ad florem solitarium reducta atque lobulis calycinis lineari-oblongis prominentibus 0.4–3.1 mm longis distinguitur.

Shrub, ca. 4 m tall; *branchlets* terete, 2–4 mm diam., glabrous; internodes not ribbed, 1.4–6.5 cm long. *Leaves* paired; linear-lanceolate to elliptic, 4–6.5 × 0.7–3.2 cm, chartaceous, glabrous; base cuneate to obtuse; apex cuspidate or acuminate; secondary veins distinct on the underside of the leaf blade, 4 to 7 pairs on each side of the costa; domatia absent; petioles 0.1–1.1 mm long, not furrowed; *stipules:* base semi-persistent or caducous, cylindrical, chartaceous, glabrous; tube 1.7–5.8 mm long, ribs forming distinct narrow wings beneath the petiole; apex entire, marcescent, 4-lobed, lobes 1.4–2.2 mm long. *Inflorescence* terminal, 1- to 3(to 9)-flowered, erect, if more than 1-flowered ± cymose, with 1 or 2 orders of branching, lax, axes glabrous; upper bracts deltate to linear or trifid, 2.5–8.6 mm long, glabrous; main axis 1.2–2.1 cm long; pedicels 2–6 mm long, glabrous. *Flowers* 5-merous; calyx cup-shaped, 2–3.2 mm wide, glabrous, hair-ring (inside calyx) absent, lobes triangular to linear, 0.4–3.1 mm long; corolla clavate in bud, white, glabrous, mature corolla unknown. *Drupes* subglobose to bi-lobed, 6.5–7.5 × 5.2–8.2 mm,

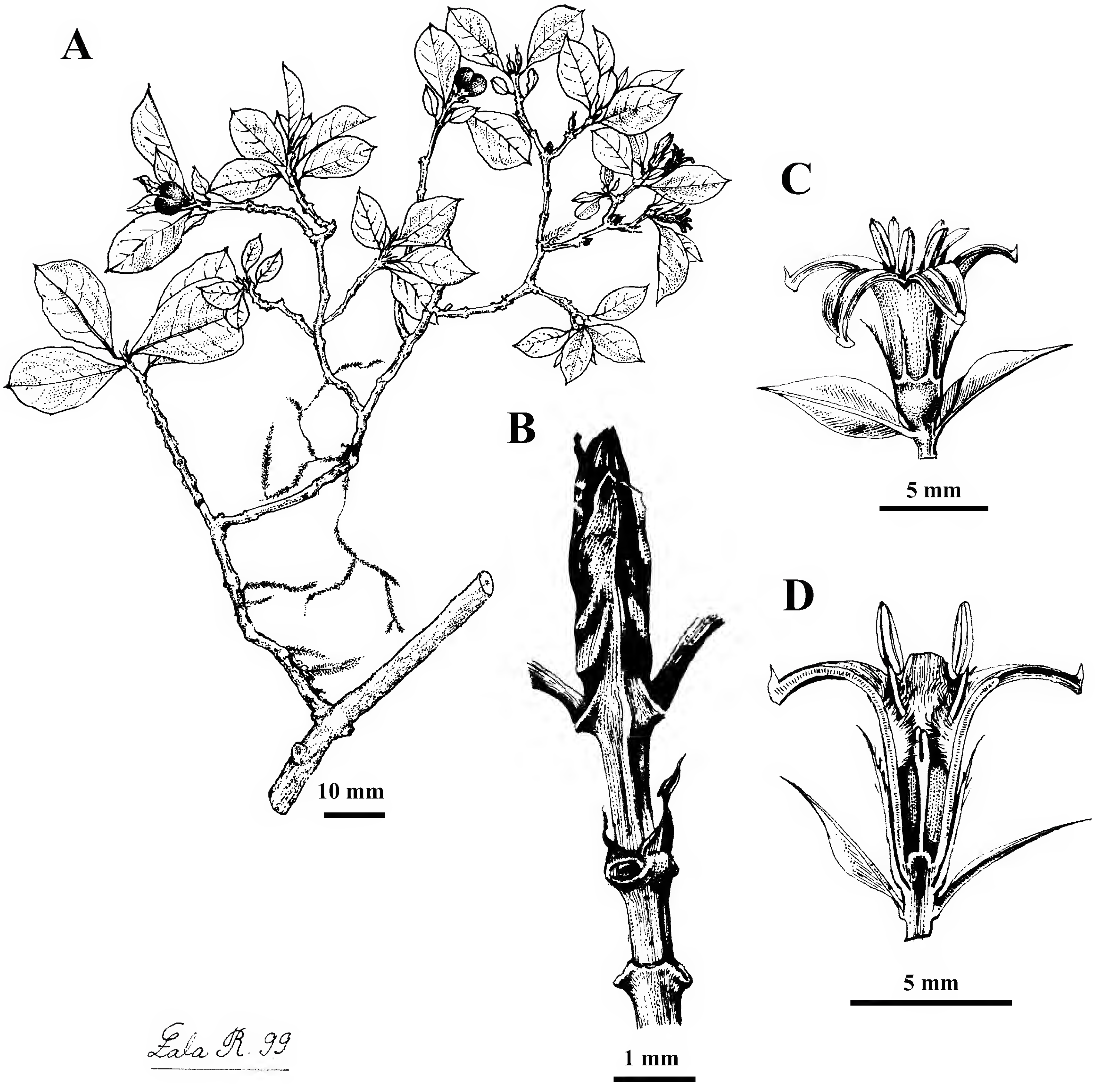
A
B
C
D
10 mm
1 mm
5 mm
5 mm
Lala R. 99

Figure 3. *Gaertnera brevipedicellata.* —A. Habit. —B. Stipules. —C. Short-styled flower. —D. Short-styled flower longitudinal section. (*Malcomber 2877,* MO, TEF.)

smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), rugose, finely fissured, endosperm ruminate.

Distribution and ecology. Madagascar, widespread but rare in Toamasina and Fianarantsoa Provinces. In evergreen humid forest, 700 to 1400 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Vulnerable VU** B1ab(i,ii,iii). B1—extent of occurrence (EOO) less than 20,000 km^2 (for *G. darcyana*: 9452 km^2); a—severely fragmented and known to exist in no more than 10 locations (for *G. darcyana*: three collections giving three geo-reference points, representing three locations); b (i–iii)—continuing decline inferred due to observed degradation of habitat.

Phenology. Flowering: November–December; fruiting unknown.

Gaertnera darcyana differs from other *Gaertnera* species treated herein by the combination of cylindrical stipules and prominent, linear calyx lobes of differing lengths. The usually 1-flowered inflorescence and linear calyx lobes of differing lengths observed in *G. darcyana* suggests an affiliation with *G. madagascariensis*. However, *G. darcyana* differs from *G. madagascariensis* in having cylindrical stipules and glabrous vegetative and sexual parts. Although *G. darcyana* usually has 1- to 3-flowered inflorescences, rarely an inflorescence with up to 9 flowers is observed. This species is named in honor of William D'Arcy, former curator at the Missouri Botanical Garden, whose important contributions include making numerous Malagasy botanical collections and pioneering taxonomic work on the Solanaceae.

Paratypes. MADAGASCAR. **Toamasina:** Ambodiniana, *G. Cours 1926* (P). **Fianarantsoa:** Haute vallée de la Rienana (Bassin du Matitanana), *H. Humbert 3566* (P).

5. **Gaertnera furcellata** (Baill. ex Vatke) S. T. Malcomber & A. P. Davis, comb. nov. Basionym: *Psychotria furcellata* Baill. ex Vatke, Abh. Naturwiss. Vereine Bremen 9: 118. 1885. TYPE: Madagascar. Without further locality information, 24 Nov. 1877, *D. C. Rutenberg s.n.* (holotype, P!).

Shrub, ca. 2 m tall; *branchlets* terete, 1–2 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.5–1.2 cm long. *Leaves* paired, elliptic, 0.5–1.2 × 0.3–0.5 cm, membranous or chartaceous, glabrous; base cuneate; apex acute (or very briefly cuspidate); secondary veins indistinct to invisible on the underside of the leaf blade, 3 or 4 pairs on each side of the costa; domatia absent; petioles absent or up to 0.3 mm long, not furrowed; *stipules* persistent or base semi-persistent (as 4 thin, membranous remnants), calyptrate, membranous, glabrous; tube ± absent or up to 1 mm long, 4 ribs forming ± distinct narrow wings around the petiole to stipule lobes; apex with 4 incisions, 4-lobed, lobes linear to filiform, 3–4 mm long. *Inflorescence* terminal and/or terminal axillary branches, 1-flowered, erect; bracteoles inserted on the pedicel, indistinct; pedicel absent or up to 1 mm long. *Flowers* 4-merous, bisexual, heterodistylous. *Long-styled flowers*: calyx campanulate, 1.5–2 mm wide, glabrous, hair-ring (inside calyx) present; lobes triangular to linear, 0.5–2.5 mm long; corolla clavate in bud, salverform when open, 2.5–3 × 1.2–1.7 mm, white, glabrous outside, inside with a ring of villous hairs in the upper third, lobes 2.2–2.8 mm long, hemi-elliptic to linear, apex acute or rounded, inside glabrous; anthers included, filaments inserted in upper third of tube, up to 0.3 mm long; style 5 mm long, glabrous, stigma 0.5–0.7 mm long. *Short-styled flowers*: unknown. *Drupes* unknown.

Distribution and ecology. Madagascar, Toamasina Province, only known from Sahamalaza. In evergreen humid forest, ca. 900 m, on metamorphic and igneous basement rocks (Fig. 2).

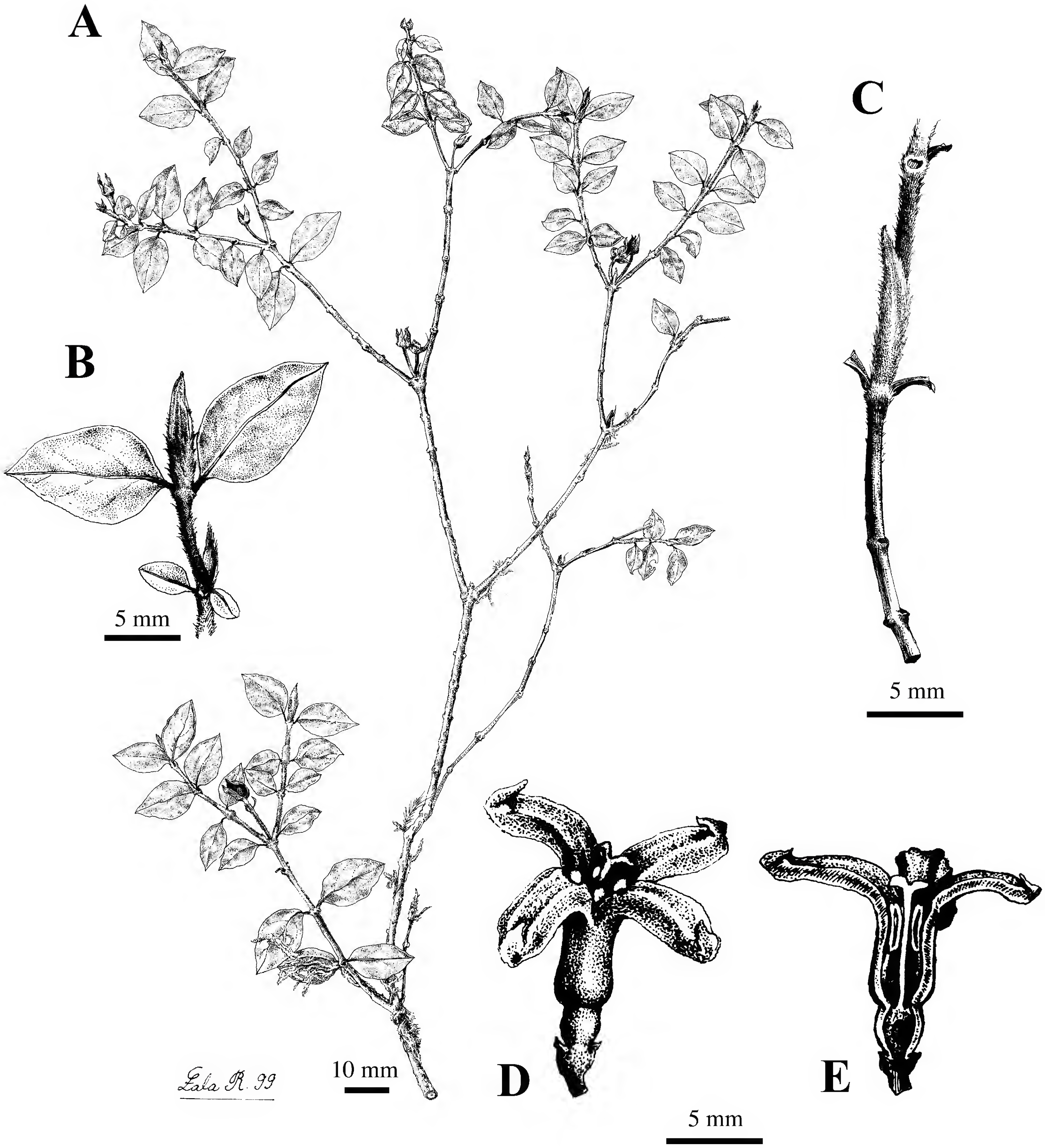
A
B
5 mm
C
5 mm
Lala R. 99
10 mm
D
E
5 mm

Figure 4. *Gaertnera madagascariensis.* —A. Habit. —B. Developing stipules. —C. Mature stipules. —D. Long-styled flower. —E. Long-styled flower longitudinal section. (*Malcomber 2870,* MO, TEF.)

Conservation status. IUCN Red List Category (IUCN, 2001): **Critically Endangered CR** B1ab(i,ii,iii)+2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 100 km^2 (for *G. furcellata*: not known, as only from a single locality); a—known to exist at only a single location (for *G. furcellata*: two collections giving one georeference point, representing one locality); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 10 km^2 (for *G. furcellata*: not known, as only from a single locality). B2ab—as for B1.

Phenology. Flowering in November; fruiting unknown.

A determination slip placed on the holotype of *Psychotria furcellata* by C. E. B. Bremekamp alerted us to the association of this taxon with *Hymenocnemis* and therefore *Gaertnera*. Bremekamp wrote "*Hymenocnemis furcellata* (Baill. ex Vatke) Brem. *n. comb.*" on the determination slip, although he did not make his proposed combination in *Hymenocnemis*. We are taking the opportunity here to make a new combination for this entity in *Gaertnera*. Vatke (1885) stated in his description of *P. furcellata* that the ovary is inferior ("*germine infero breviter obconico*"), although comparison of material (*J. Dequaire 27977*, K) matched with the holotype shows that it is superior. There was not sufficient material of the holotype to make a floral dissection. Stipule and branchlet morphology (see description, above) alone clearly supports the placement of this taxon in *Gaertnera*.

Gaertnera furcellata is a poorly known species, known from only three collections, one of which (the holotype) is without locality data. This species can be separated from most other *Gaertnera* species due to the presence of unusual lacerated calyptrate stipules, which persist as four membranous remnants at the leaf node. These unusual stipules are present in only one other species, viz. *G. microphylla*. *Gaertnera furcellata* differs from *G. microphylla* by its elliptic to narrowly elliptic leaves versus obovate to spathulate leaves in *G. microphylla*.

According to Vatke (1885) a specimen collected by the Rev. R. Baron (*R. Baron 1077*, K) belongs to *Psychotria furcellata* (" *= Baron 1077 in hab. kew.* [sic] *stipulis delapsis*"). On the typed copy of Vatke's protologue attached to the holotype of *P. furcellata*, which was almost certainly made by Bremekamp, there is a note stating that *Baron 1077* represents *Saldinia myrtilloides* Bremekamp var. *angustifolia* (see also Bremekamp, 1957: 128). We concur with Bremekamp on the placement of this specimen.

Specimens examined. MADAGASCAR. **Toamasina:** Samalahaza, Ambatondrazaka, *G. Cours 1203 or O. 307* (K, P); Samalahaza, *J. Dequaire 27977* (K, P).

6. Gaertnera madagascariensis (Hook. f.) S. T. Malcomber & A. P. Davis, comb. nov. Basionym: *Hymenocnemis madagascariensis* Hook. f., Gen. Pl. 2: 133. 1873. TYPE: Madagascar. Without precise locality, *W. Bojer s.n.* (holotype, K!). Figure 4.

Tree, 2–5 m tall; *branchlets* terete, 0.4–3 mm diam., young branchlets pubescent, indumentum gray-white or brown to orange, older branchlets glabrous or puberulent to pubescent, indumentum gray or brown; internodes not ribbed, 0.4–2.5 cm long. *Leaves* paired, ovate or sometimes ovate-elliptic, 0.5–4 × 0.3–2.5 cm, chartaceous, glabrous; base obtuse or rounded; apex acute; secondary veins distinct on the underside of the leaf blade, 3 to 5(or 6) pairs; domatia present in axils between costa and secondary veins, densely pubescent; petioles 0.5–2.5 mm long, not furrowed; *stipules* caducous, adnate and tubular for most of their length, calyptrate, membranous, pubescent; tube 3.8–12.1 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with a single interpetiolar cleft, the 2 lobes deltate to triangular, 0.3–0.6 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1(to 3)-flowered, if more than 1-

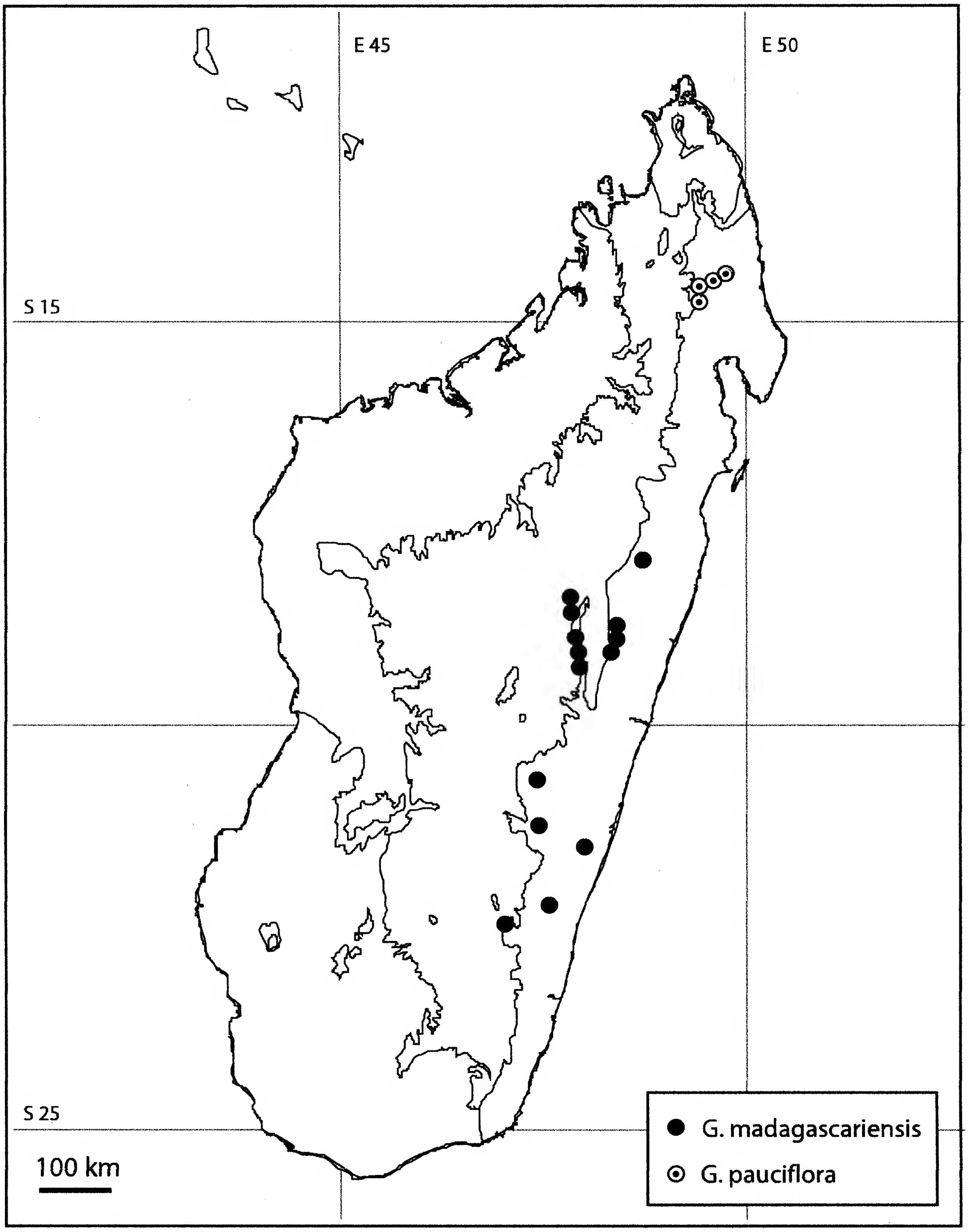
E 45
E 50
S 15
S 25
100 km
● G. madagascariensis
⊙ G. pauciflora

Figure 5. Distribution of *Gaertnera madagascariensis* and *G. pauciflora* mapped on the bioclimatic zones of Madagascar.

flowered ± cymose, lacking branches, sessile (peduncle absent), erect, lax; axes pubescent or puberulent; upper bracts narrowly triangular, up to 5 mm long, glabrous or puberulent; bracteoles absent; pedicels 2.5–12 mm long, pubescent. *Flowers* 4- or 5-merous; *long-styled flowers*: calyx campanulate, 1.2–2.5 mm wide, glabrous, hair-ring (inside calyx) absent, lobes narrowly triangular to linear, 0.5–4 mm long; corolla clavate in bud, salverform when open, 5–13.2 × 3.2–18.5 mm, white, outside and inside glabrous, lobes 3–5 mm long, hemi-elliptic to oblong, apex acute, glabrous inside; anthers included, filaments inserted in upper third of tube, 0.1–0.4 mm long; style 7–10 mm long, glabrous, stigma 0.3–0.7 mm long; *short-styled flowers* unknown. *Drupes* globose or subglobose, 5–6 × 5–6 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) to hemispherical (2 pyrenes), rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar: Antananarivo, Fianarantsoa, and Toamasina Provinces. In evergreen humid forest, 800 to 1400 m, primarily on metamorphic and igneous basement rocks, but one collection on alluvial and lake deposits (Fig. 5).

Phenology. Flowering November–March; fruiting March–May.

Conservation status. IUCN Red List Category (IUCN, 2001): **Least Concern LC**. Extent of occurrence (EOO) more than 20,000 km^2 (for *G. madagascariensis*: 41,773.5 km^2); known from at least 10 locations (7 present in protected areas); area of occupancy (AOO) more than 2000 km^2 (for *G. madagascariensis*: 16,954 km^2).

Transfer of *Hymenocnemis madagascariensis* completely subsumes the monotypic *Hymenocnemis* genus within *Gaertnera* (see above). Of the characters used by Hooker (1873) to diagnose *Hymenocnemis* that are variable within *Gaertnera*, calyptrate stipules that cap the growing tip are also found in five of the usually 1-flowered *Gaertnera* species included in this contribution (*G. alata*, *G. brevipedicellata*, *G. furcellata*, *G. microphylla*, and *G. pauciflora*). As in *G. madagascariensis*, the new species *G. brevipedicellata* and *G. pauciflora* also have 4- or 5-merous flowers. In contrast, *G. bambusifolia* and *G. darcyana* have exclusively 5-merous flowers, and *G. alata*, *G. furcellata*, and *G. microphylla* have exclusively 4-merous flowers. In addition to *G. madagascariensis*, unequal calyx lobes can be found in *G. darcyana*. Of the other species with usually 1-flowered inflorescences, only *G. pauciflora* has anthers with prominent apical appendages similar to those found in *G. madagascariensis* (although mature flowers of *G. bambusifolia* are unknown). *Gaertnera madagascariensis* is diagnosed by the combination of 1(or occasionally 3)-flowered inflorescences, densely pubescent young branchlets, and caducous, membranous stipules.

Additional specimens examined. MADAGASCAR. **Antananarivo:** Anjozorobe, *J. Bosser 12839* (K, P, TAN), *J. Bosser 8200* (TAN); Ankeramadrinka, Ambatolaona, *J. Leandri 3204* (P); Andrangoloaka, Aug. 1881, ***G. Parker s.n.*** (K); Tsiazompaniry, Andapa, *R. Capuron SF-20287* (K, P). **Fianarantsoa:** Ambohimitombo (Tanala), *C. Forsyth-Major 317* (K), *401a* (K); Andringitra massif, Ambodipaiso forest, *G. Cours 2286* (P), *A. Homolle 2286* (P, TAN); Farafangana, Ivongo, *C. Rakotovao RN-8518* (P); High valley of Rienana (Matitanana basin), *J. Humbert 3578* (P); Ranomafana National Park, Vatoharanana, *S. Malcomber 2865* (MO, TEF), *S. Malcomber 2870* (MO, TEF). **Toamasina:** Analamazoatra, *H. Perrier de la Bâthie 6892* (K, P); Anosibe to Andapabe, *G. Cours 4425* (P, TAN); Bemainty massif, Rahobevava, *G. Cours 4177* (P, TAN); Col de Saharanga, *R. Capuron SF-24027* (MO, P); Crête de l'Ampahana, *R. Capuron SF 28774* (TEF); Moramanga-Anosibe, pk 29, *J. Bosser 6722* (P); Sandrangato and Anosibe (S of Moramanga), *R. Capuron 1641* (P); Analabe, *H. Perrier de la Bâthie 18527* (P); Koubaville, *R. Capuron SF-24413* (MO, P); Rahobevava, *G. Cours 4363* (P, TAN); Tsiazompaniry, Andapa, *R. Capuron SF-20287* (K, P).

7. **Gaertnera microphylla** Capuron ex S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Toamasina: 6.6 km SE of Andasibe, small ridge beside RN2 at base of Andriandavibe, 18°56′S, 48°29′E, 23 Nov. 1997, S. *Malcomber, A. Davis, D. Gower & J. Andriantiana 2925* (holotype, MO!; isotypes, A!, BR!, G!, K!, LE!, MAL!, MAU!, P!, PRE!, TEF!, UPS!, WAG!). Figure 6.

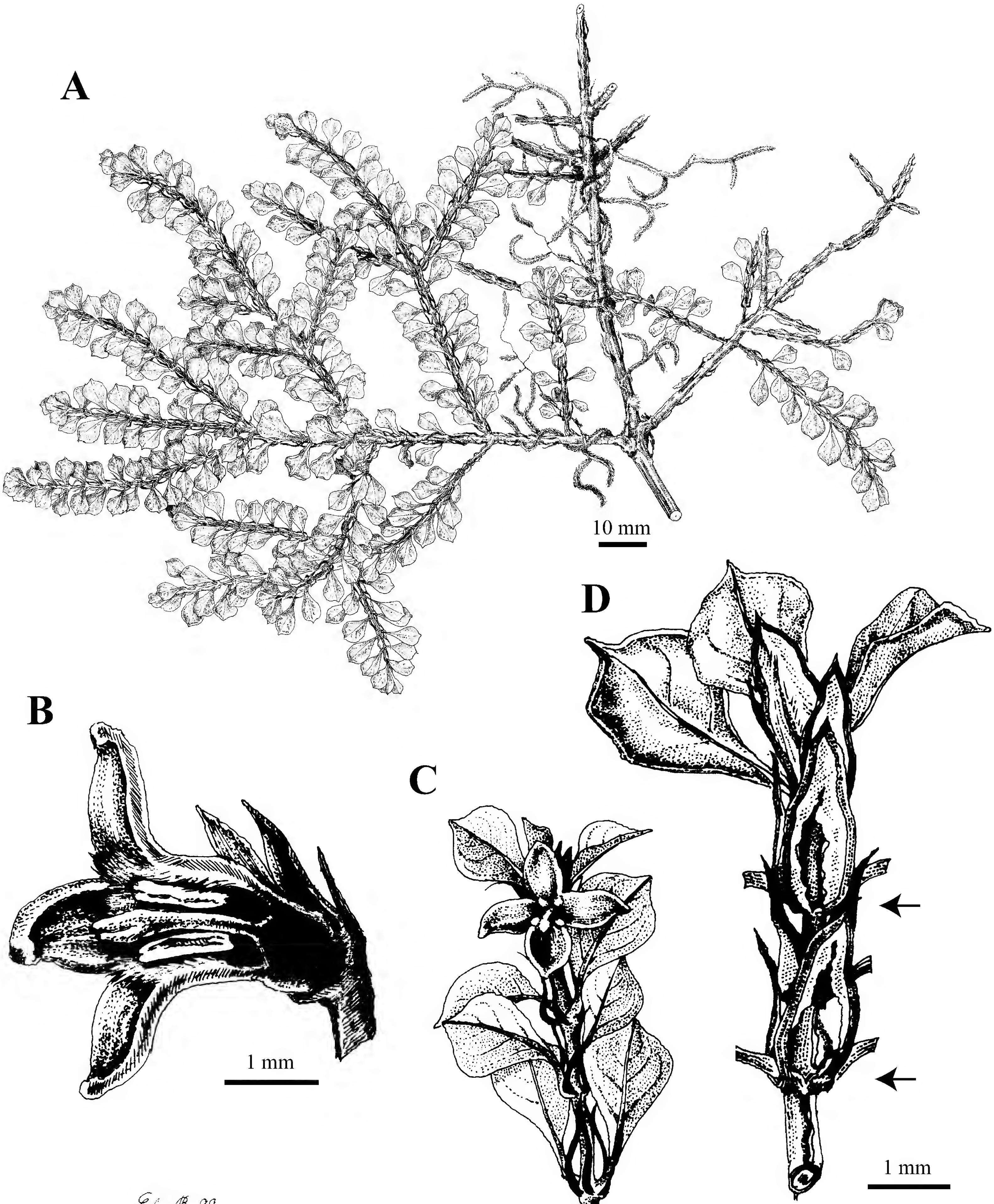
A
10 mm
D
B
C
1 mm
1 mm
1 mm
Lala R. 99

Figure 6. *Gaertnera microphylla*. —A. Habit. —B. Long-styled flower longitudinal section. —C. Fertile branch. —D. Sterile branch with developing stipules (see arrows). (*Malcomber 2925*, MO, TEF.)

Haec species *Gaertnerae madagascariensi* similis, sed ab ea planta omnino glabra, foliis obovatis vel spathulatis mucronulatis atque stipulis pro laciniis quattuor membranaceis tenuis persistentibus distinguitur.

Tree or shrub, 2–4 m tall; *branchlets* terete, 0.4–3.4 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.1–0.6 cm long. *Leaves* paired; obovate to spathulate, 0.3–1.5 × 0.3–0.8 cm, membranous, glabrous; base attenuate; apex mucronulate; secondary veins barely visible on the underside of the leaf blade, 3 or 4 pairs on each side of the costa; domatia absent or present in axils between costa and secondary veins, glabrous or densely pubescent; petioles 0.5–1.2 mm long, not furrowed; *stipules:* base semi-persistent (as 4 thin, membranous remnants), calyptrate, membranous, glabrous; tube up to 1 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with 4 incisions, 4-lobed, lobes linear, 3–5 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1-flowered, erect; bracteoles absent; pedicel indistinct. *Flowers* 4-merous; *long-styled flowers*: calyx cup-shaped, 1.5–2 mm wide, glabrous, hair-ring (inside calyx) absent, lobes linear to hemi-elliptic, 2.4–3 mm long; corolla clavate in bud, salverform when open, 4–4.5 × 1.5–3 mm, white, outside glabrous, inside villous hairs in about the middle, lobes 2–2.5 mm long, triangular to hemi-elliptic, apex obtuse, inside glabrous; anthers included, filaments inserted in upper third of tube, 0.2–0.4 mm long; style 4.5–5 mm long, glabrous, stigma 0.9–1.3 mm long; *short-styled flowers*: unknown. *Drupes* bi-lobed, 5–6.2 × 6.5–7 mm, smooth, blue, glabrous; 2 pyrenes per drupe, hemispherical, rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Toamasina Province, restricted to environs around Andasibe and Analamazoatra. In evergreen humid forest, 790 to 900 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Critically Endangered CR** B1ab(i,ii,iii)+2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 100 km^2 (for *G. microphylla*: 34 km^2); a—severely fragmented throughout range (for *G. microphylla*: five collections giving three geo-reference points, representing three localities); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 10 km^2 (for *G. microphylla*: 3.3 km^2 based on three cells of 1.0 km^2); B2ab—as for B1.

Phenology. Flowering November–December; fruiting January–May.

René Capuron first applied the name *Gaertnera microphylla* to specimens he collected in the 1960s from the environs of Andasibe, which are deposited in the TEF herbarium. In 1951 C. E. B. Bremekamp wrote "*Hymenocemis parviflora* Brem. sp. nov." on a specimen held in the Paris Herbarium (*H. Perrier de la Bâthie 6893*, P). This epithet cannot be taken up as it has already been used in *Gaertnera* (*G. parviflora* Bojer).

Gaertnera microphylla and *G. furcellata* share calyptrate stipules that persist as four membranous remnants at the leaf node. Both species are morphologically isolated within *Gaertnera* and are diagnosed by the stipule morphology and cymes reduced to a single flower. *Gaertnera microphylla* differs from *G. furcellata* in having obovate to spathulate leaves.

Paratypes. MADAGASCAR. **Toamasina:** between Perinet and Anevoka, base de rocher d'Andriandavibe, ***R. Capuron SF 24355*** (MO, P, TEF), ***R. Capuron SF 24770*** (MO, P, TEF); region of Saharanga mountain pass, NE of Perinet, ***R. Capuron SF 24022*** (MO, P, TEF); Analamazoatra, ***H. Perrier de la Bâthie 6893*** (P).

8. Gaertnera pauciflora S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antsiranana: E of Andapa, Marojejy Nature Reserve (RNI # 12), above camp #3, 14°26'13"S, 49°44'36"E, 1300–1500 m, 19–20 Sep. 1997, *S. Malcomber 2781* (holotype, MO!; isotypes, A!, BR!, G!, K!, LE!, MAL!, MAU!, P!, PRE!, TEF!, WAG!). Figure 7.

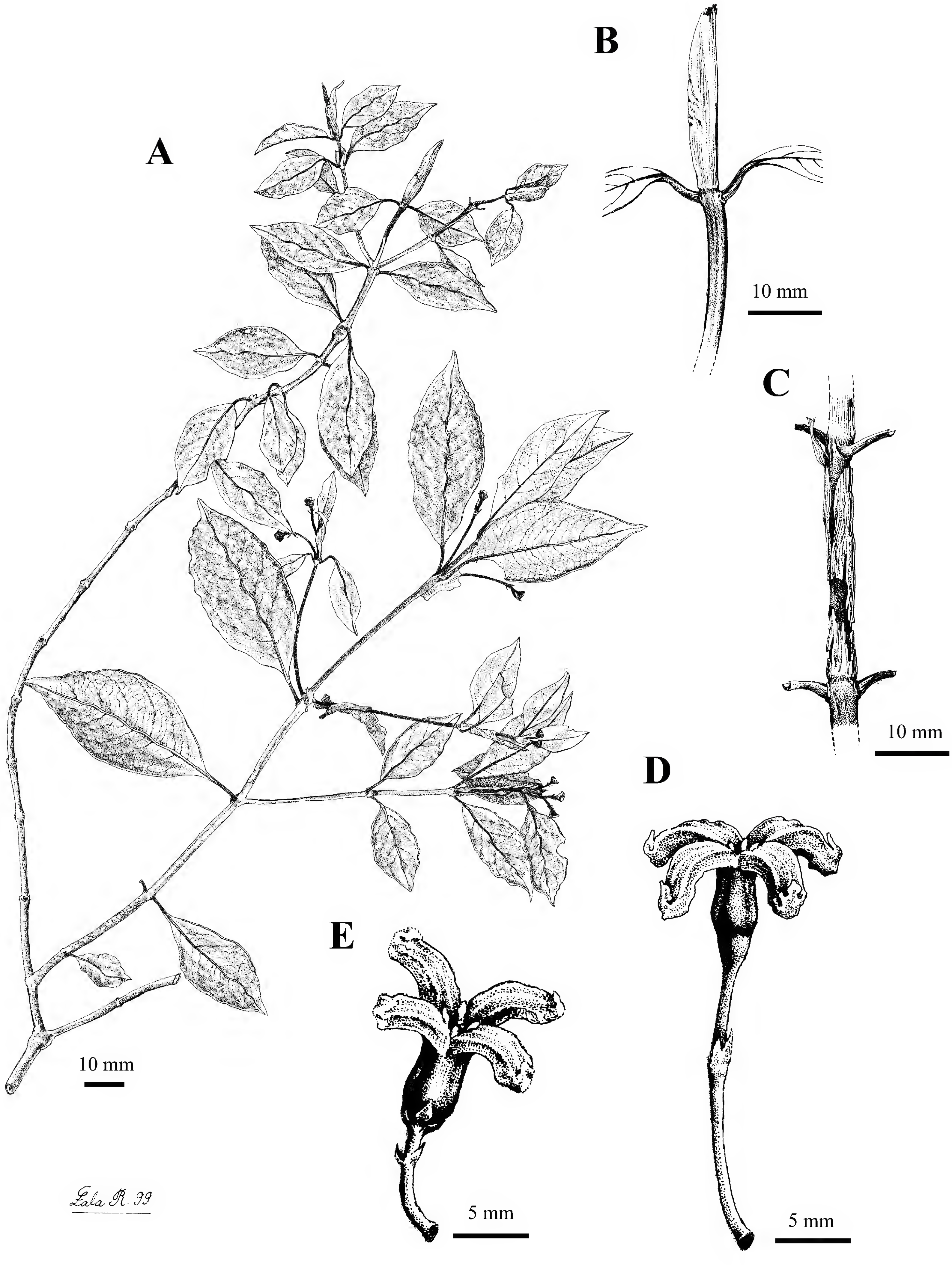
A
B
C
D
E
10 mm
10 mm
10 mm
5 mm
5 mm
Lala R. 99

Figure 7. *Gaertnera pauciflora.* —A. Habit. —B. Developing stipules. —C. Mature stipules. —D. Short-styled flower. —E. Long-styled flower. (*Malcomber 2780,* MO, TEF.)

Haec species *Gaertnerae obovatae* similis, sed ab ea inflorescentia ad florem solitarium vel raro ad cymam trifloram reducta, pedicello prominenti 2.5–9.1 mm longo atque tubo corollino 4–7.5 mm longo distinguitur.

Tree or shrub, 1.5–6 m tall; *branchlets* terete, 1–3 mm diam., glabrous or sparsely pubescent; internodes with 2 longitudinal ribs, 0.4–2.6 cm long. *Leaves* paired; elliptic to oblanceolate, 1–4.5 × 0.4–2 cm, chartaceous, glabrous; base attenuate or cuneate; apex abruptly cuspidate or acute; secondary veins distinct on the underside of the leaf blade, 4 to 6 pairs on each side of the costa; domatia absent or present in axils between costa and secondary veins, pubescent; petioles 1.5–3 mm long, not furrowed; *stipules* calyptrate, caducous, membranous, glabrous or pubescent; tube 10–21 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with a single interpetiolar cleft or with 2 opposite incisions, 2-lobed, lobes deltate, up to 0.5 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1(to 3)-flowered, if more than 1-flowered ± cymose, lacking axes, sessile (peduncle absent), erect, lax; upper bracts absent, bracteoles inserted on the pedicel, indistinct; pedicels 2.5–9.1 mm long (occasionally borne on slender peduncles), glabrous. *Flowers* 4- or 5-merous; *long-styled flowers*: calyx cup-shaped, 1–3 mm wide, glabrous, hair-ring (inside calyx) absent, lobes triangular, 0.2–0.4 mm long; corolla clavate in bud, salverform when open, 4–7.5 × 2.5–3 mm, white glabrous outside and inside; lobes 6–8 mm long, hemi-elliptic to linear, apex acute, inside glabrous; anthers included, filaments inserted in lower third of tube, 0.2–1 mm long; style 5–6 mm long, glabrous, stigma 0.5–1 mm long; *short-styled flowers*: calyx cup-shaped, 1.2–2.8 mm wide, glabrous, hair-ring (inside calyx) absent; lobes triangular, 0.1–0.3 mm long; corolla clavate in bud, salverform when open, white, 4–7.5 × 2.5–3 mm, glabrous outside and inside, lobes 6–7 mm long, hemi-elliptic or linear, apex acute, inside glabrous; anthers included, filaments inserted in lower third of tube, 1.5–2.5 mm long; style 1.8–2.5 mm long, glabrous, stigma 0.5–1.2 mm long. *Drupes* subglobose to bi-lobed, 6–7 × 5–7.5 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), ± rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Antsiranana and Majunga Provinces. In evergreen humid forests, 750 to 1500 m, on metamorphic and igneous basement rocks (Fig. 5).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN** B1ab(i,ii,iii) +2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 5000 km^2 (for *G. pauciflora*: 491 km^2); a—severely fragmented, number of collections one more than EN criteria (for *G. pauciflora*: eight collections giving six geo-reference points, representing six locations); b (i–iii)—continuing decline projected due to inferred degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km^2 (for *G. pauciflora*: 82.5 km^2 based on five cells of 4.1 km^2); B2ab—as for B1.

Phenology. Flowering September–March; fruiting October–March.

Gaertnera pauciflora is named for the one-flowered inflorescence typical of the species. *Gaertnera pauciflora* differs from other *Gaertnera* species with one-flowered inflorescences by a combination of smooth internodes, glabrous vegetative and sexual parts, calyptrate stipules, and more or less truncate calyx.

Paratypes. MADAGASCAR. **Antsiranana:** E of Andapa, Marojejy Nature Reserve (RNI #12), above camp #3 summit trail, *S. Malcomber 2779* (MO, TEF); western slopes Mt. Beondroka, *J. Miller 4483* (MO); Lokoho valley, Mt. Beondroka, N of Maroambihy, *H. Humbert 23506* (MO, P); valley of the Ambatoharanana, upper Antsahaberoka basin, *H. Humbert 31885* (P); Andapa, Ambodiangezoka, Fok. Antanambe, Foret de Betaolana, 11 km NW of Ambodiangezoka, *P. Rakotomalaza & D. Ravelomanantsoa 1985* (G, MO). **Majunga:** Befanfriana-Nord, Fir. Mantsodaka, Fok. Manandriana, Foret d'Analabe, W of Anjanaharimbe-Sud, *P. Rakotomalaza, D. Ravelonarivo & J. Ramboavelo 2044* (G, MO); Befanfriana-Nord, Fir. Mantsodaka, Fok. Manandriana, Foret d'Analabe, W of Anjanaharimbe-Sud, *P. Rakotomalaza, D. Ravelonarivo & J. Ramboavelo 2053* (G, MO).

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A REEXAMINATION OF *COFFEA* SUBGENUS *BARACOFFEA* AND COMMENTS ON THE MORPHOLOGY AND CLASSIFICATION OF *COFFEA* AND *PSILANTHUS* (RUBIACEAE–COFFEEAE)

Aaron P. Davis, Diane Bridson, and Franck Rakotonasolo

ABSTRACT. A morphological reappraisal of *Coffea* subg. *Baracoffea* shows that the present characterization of this subgenus is erroneous. An updated morphological circumscription is proposed, and several new characteristics are identified. In particular, the architecture of the flowering shoot and the gross morphology of the inflorescence are elucidated. The revised characterization shows that there are a large number of morphological differences between *Coffea* subg. *Baracoffea* and *Coffea* subg. *Coffea*. On the basis of gross morphology, the systematic position of *Coffea* subg. *Baracoffea* cannot be determined: shoot architecture and inflorescence morphology support a relationship with the genus *Psilanthus*, specifically *Psilanthus* subg. *Afrocoffea*, whereas floral morphology (along with pollen data) infers a relationship with *Coffea* subg. *Coffea*. A morphological review of *Psilanthus* and *Coffea* identified a number of potentially informative characters for assessing infrageneric relationships and showed that *Psilanthus* subg. *Psilanthus* differs quite markedly from *Psilanthus* subg. *Afrocoffea* in its vegetative and inflorescence morphology. *Coffea rhamnifolia* (*Coffea* subg. *Baracoffea*) and *Psilanthus melanocarpus* (*Psilanthus* subg. *Afrocoffea*) are identified as species of uncertain taxonomic position.

Key words: *Coffea*, *Coffea* subg. *Baracoffea*, coffee, Coffeeae, Madagascar, morphology, palynology, *Paracoffea*, *Psilanthus*.

The tribe Coffeeae DC. consists of *Coffea* L. and *Psilanthus* Hook.f. (Robbrecht & Puff, 1986), two genera that occur naturally in the Old World tropics. This tribal circumscription is chiefly characterized by the presence of 2-carpellate ovaries, each with a single ovule, axile placentation, a hard (horny/crustaceous) endocarp, seeds with a deep L- or T-shaped ventral groove (endocarp and seed-coat invaginated), a seed coat exotesta consisting of thin elongated parenchymatic cells (usually containing many more or less isolated fibers), and (2–)3–5-colporate (zonocolporate) pollen (derived from: Robbrecht, 1981; Robbrecht & Puff, 1986; Stoffelen et al., 1997). The Asiatic genus *Nostolachma* T. Durand (= *Lachnostoma* Korth.), previously associated with Coffeeae by Leroy (1980b), was excluded from the tribe by Robbrecht and Puff (1986).

Studies by Andreasen and Bremer (1996, 2000) and Andreasen et al. (1999) have provided molecular evidence for an enlarged concept of the Coffeeae, to include genera formerly placed in Gardenieae subtribe Diplosporinae (Robbrecht & Puff, 1986; Robbrecht, 1988, 1994), including *Tricalysia* A. Rich., *Diplospora* DC., and *Discospermum* Dalzell. The genus *Bertiera* Aubl. (Gardenieae subtribe Gardeniinae, fide Robbrecht (1994) or Gardenieae subtribe Bertierinae fide Bridson (1998)) is also convincingly associated with the Coffeeae (Andreasen et al., 1999; Andreasen & Bremer, 2000). Molecular investigations by Persson (2000) independently support a wider concept for Coffeeae, and Vinckier et al. (2000) showed that the same pollen orbicule type (Type VI) is found in *Coffea, Psilanthus, Tricalysia,* and *Bertiera*, but no other members of subfamily Ixoroideae.

In this study we have restricted our investigations to what we term as the "core Coffeeae," which is equivalent to Coffeeae sensu Robbrecht and Puff (1986) and Robbrecht (1988, 1994), i.e., *Coffea* and *Psilanthus*. Recent systematic data (e.g., Andreasen & Bremer, 2000) support a convincing sister relationship between *Coffea* and *Psilanthus*, although taxon sampling of the "core Coffeeae" and Coffeeae (fide Andreasen & Bremer, 2000) has so far been confined to relatively few taxa.

Psilanthus is divided into two subgenera: subg. *Psilanthus* and subg. *Afrocoffea* (Moens) Bridson. *Psilanthus* subg. *Psilanthus* contains two species, *P. mannii* Hook.f. and *P. sapinii* De Wild., which occur in tropical central and western Africa. *Psilanthus* subg. *Afrocoffea* comprises ca. 20 species and occurs in Africa, Asia, and Australasia; it is absent from Madagascar and the Mascarenes. The genus *Paracoffea* J.-F. Leroy (Leroy, 1967), which is often cited during studies of the Coffeeae (e.g., Andreasen & Bremer, 1996; Vinckier et al., 2000) is a synonym of *Psilanthus* (Davis, 2003).

Coffea is divided into two subgenera: subg. *Coffea* and subg. *Baracoffea* (J.-F. Leroy) J.-F. Leroy. *Coffea* subg. *Coffea* comprises ca. 90 species and occurs naturally throughout tropical Africa, Madagascar, and the Mascarenes; it contains the three species used in the production of the beverage coffee (*C. arabica* L., *C. canephora* A. Froehner, and *C. liberica* Hiern) and is thus comparatively well known. Conversely, *Coffea* subg. *Baracoffea* is a small (fewer than 8 spp.) and poorly known subgenus, from western Madagascar, Kenya, and Somalia. Although species of *Coffea* subg. *Baracoffea* have not been included in molecular systematic studies, preliminary molecular data (O. Maurin, pers. comm.) support the inclusion of *Coffea* subg. *Baracoffea* within the "core Coffeeae."

The monospecific *Coffea* subg. *Psilanthopsis* (A. Chev.) J.-F. Leroy (1980a) is no longer recognized as separate from *Coffea* subg. *Coffea* (Bridson, 1994: 340).

Coffea subg. *Baracoffea* is currently represented (fide Leroy, 1980a, 1982) by three named species from western Madagascar (*C. decaryana* J.-F. Leroy, *C. grevei* Drake ex A. Chev. (= *C. capuronii* J.-F. Leroy and *C. morondavensis* J.-F. Leroy; in syn., in sched. P, fide J.-F. Leroy), and *C. humbertii* J.-F. Leroy). According to Leroy (1982), *C. rhamnifolia* (Chiov.) Bridson (syn. *C. paolia* Bridson), from Kenya and Somalia, also belongs in *Coffea* subg. *Baracoffea*. Bridson (1987) initially accepted Leroy's placement but later (Bridson, 1988a, 1988b) expressed doubts, because of similarities in flower and fruit morphology between *C. rhamnifolia* and *Coffea* subg. *Coffea*. Bridson (1982: 853, 1988a) noted that *C. rhamnifolia* seems to form a morphological link between *Coffea* and *Psilanthus*.

According to Leroy (1961, 1980a, 1980b, 1982), *Coffea* subg. *Baracoffea* is characterized by: a shrub life-form; sympodial development; persistent [evergreen] or deciduous (Leroy, 1961) leaves; terminal, one-flowered inflorescences with one to three pairs of leaves; inflorescences possessing cataphylls but without calyculi or bracteoles; relatively short corolla tubes; long styles; versatile filaments ('non-sessiles' fide Leroy, 1980a); anthers exserted or semi-exserted; bacciform fruits; and seeds either devoid of or with small amounts of caffeine.

Leroy's circumscription of *Coffea* subg. *Baracoffea* has not hitherto been challenged, partly, at least, because so little material has been available until the present time. Preliminary study of herbarium specimens (Davis & Bridson, pers. obs.) identified problems with Leroy's characterization (Leroy, 1980a, 1980b, 1982) but further significant improvement was hampered due to the paucity of available study material. Between 1998 and 2000, however, two of us (Davis & Rakotonasolo, pers. obs.) had the opportunity to visit various locations in Madagascar to study *Coffea* subg. *Baracoffea* in situ. The results of the fieldwork and further study of collected material has enabled a morphological reappraisal of *Coffea* subg. *Baracoffea*, which is reported here in this contribution. Our studies have also revealed the presence of four new species from western Madagascar, which appear to belong to *Coffea* subg. *Baracoffea*.

Overviews of the classification and nomenclatural history of *Psilanthus* and *Coffea* are provided by Bridson (1987, 1988b) and Stoffelen (1998). A synopsis of the subgeneric classification for these two genera after Bridson (1988b) is given in Table 1. Appendix 2 contains representative species lists for *Coffea* subg. *Coffea* and *Psilanthus*, and a complete list of species for *Coffea* subg. *Baracoffea*.

TABLE 1.

Genera and subgenera of *Coffea* and *Psilanthus* (modified from Bridson, 1988b), including type species, number of species, geographical distribution, and relevant synonyms.

Coffea L. Sp. Pl.: 172. 1753.

Coffea subg. **Coffea** L. Type species: *Coffea arabica* L. Around 90 species. Africa, Madagascar, Mascarenes.

Coffea subg. *Psilanthopsis* (A. Chev.) J.-F. Leroy, Assoc. Sci. Int. Café, (ASIC) 9th Colloque: 475. 1980. *Psilanthopsis* A. Chev., J. Agric. Trop. Bot. Appl. 19: 404. 1939. Type species: *Coffea kapakata* (A. Chev.) Bridson. Monotypic. Africa (Angola).

Coffea subg. **Baracoffea** (J.-F. Leroy) J.-F. Leroy, Assoc. Sci. Int. Café, (ASIC) 9th Colloque: 475. 1980. *Coffea* sect. *Baracoffea* J.-F. Leroy, Compt. Rend. Hebd. Séances Acad. Sci. 252: 2287. 1961. Type species: *Coffea humbertii*. Four species (including *C. rhamnifolia*) and four undescribed species. Madagascar and Somalia and Kenya (if including *C. rhamnifolia*).

Paolia Chiov., Result. Sci. Miss. Stef.-Paoli, Coll. Bot. 1: 93. 1916. Type species: *Paolia jasminoides* Chiov. (= *C. rhamnifolia* (Chiov.) Bridson). Monotypic. Africa (Somalia & Kenya).

[*Paracoffea* subg. *Insulanoparacoffea* J.-F. Leroy, J. Agric. Trop. Bot. Appl. 14: 276. 1967, nom. nud.]

Psilanthus Hook.f., Gen. Pl.: 115. 1873.

Psilanthus subg. **Psilanthus** Hook.f. Type species: *Psilanthus mannii* Hook.f. Two species. Africa (central & western).

Psilanthus subg. **Afrocoffea** (Moens) Bridson, Kew Bull. 42: 454. 1987. *Coffea* subg. *Afrocoffea* Moens, Bull. Jard. Bot. État. 32: 131. 1962. Type species: *Psilanthus lebrunianus* (R. Germ & Kesler) J.-F. Leroy ex Bridson. Around 17 species. Africa, Asia, Australasia.

Coffea sect. *Paracoffea*. Miq., Fl. Ind. Batavae: 308. 1856. *Paracoffea* J.-F. Leroy, J. Agric. Trop. Bot. Appl. 14: 276. 1967. *Psilanthus* subg. *Paracoffea* (Miq.) J.-F. Leroy, Assoc. Sci. Int. Café, (ASIC) 9th Colloque: 475. 1980. *Paracoffea* J.-F. Leroy, J. Agric. Trop. Bot. Appl. 14: 276. 1967. Type species: *Coffea horsfieldiana* Miq.

[*Paracoffea* subg. *Afroparacoffea* J.-F. Leroy, J. Agric. Trop. Bot. Appl. 14: 276. 1967, nom. nud.]

[*Paracoffea* subg. *Melanoparacoffea* J.-F. Leroy, J. Agric. Trop. Bot. Appl. 14: 276. 1967, nom. nud.]

MATERIAL AND METHODS

Field studies in Madagascar were undertaken by Davis and Rakotonasolo in 1998, 1999, and 2000, and by Rakotonasolo in 1999 and 2000. Investigations of herbarium specimens were undertaken at Antananarivo (TAN and TEF), Leiden (L), Paris (P), and Kew (K). Further material was loaned from Missouri (MO), Wageningen (WAG), and Geneva (G) and studied at Kew. A list of representative material examined is given in Appendix 2.

Pollen grains were acetolyzed following the method of Erdtman (1960) and mounted in glycerol jelly. For light microscopy a Nikon Optiphot microscope was used, fitted with a CF Plan Apochromat objective (100x, NA 1.40), and compensating ×10 eyepieces. Ten pollen grains were measured for pollen size (polar length and equatorial width), polar exine thickness, colpus length, and aperture shape and width. For scanning electron microscopy (SEM) acetolyzed pollen grains were transferred into 95% ethanol, pipetted onto aluminium stubs, previously cleaned in acetone in an ultrasonic bath. The pollen suspensions on the aluminium stubs were covered with an inverted glass beaker and left to evaporate at room temperature. The stub preparations were coated with ca. 90nm of platinum in a Balzer's SCD 030 sputter coater, and examined with a Hitachi S2400 SEM.

All species of *Coffea* subg. *Baracoffea* were examined for this study, including four undescribed species identified here as *C.* sp. nov. 1–4. For the morphological review of other "core Coffeeae" we examined a broad selection of species from *Coffea* subg. *Coffea* and *Psilanthus* subg. *Afrocoffea*. For *Psilanthus* subg. *Psilanthus*, only *P. mannii* was examined; for information on the little-known *P. sapinii* De Wild. we relied on the work of Stoffelen (1998: 139). *Psilanthus sapinii* shares the same major morphological features as *P. mannii*, although the flowers of *P. sapinii* are unknown. *Psilanthus melanocarpus* (Hiern) J.-F. Leroy (*Psilanthus* subg. *Afrocoffea*) is treated independently in our observations and discussions because the morphology of this species differs markedly from other species in the same subgenus. *Coffea rhamnifolia* is treated in a similar manner because the systematic position of this species within *Coffea* subg. *Baracoffea* is debatable (Bridson, 1982, 1988a).

Cladistic analyses were performed using PAUP* version 4.0b4a (PPC) written by David L. Swofford. Branch and Bound searches (more than six taxa) were performed using Fitch optimization, with 1000 random sequence additions and TBR (tree bisection-reconnection) branch swapping and MULPARS options. Exhaustive searches (six taxa, or less) were performed using the PAUP* default settings. Internal tree support was evaluated using the bootstrap method (Felsenstein, 1985) with 10,000 replicates, full heuristic search, random taxon addition, and TBR branch swapping.

RESULTS

Our morphological reassessment of *Coffea* subg. *Baracoffea* shows that the present characterization of the subgenus (Leroy, 1980a, 1982) is unsatisfactory. Our amended characterization is as follows, with Leroy's characters given in parentheses. A full explanation of all characters listed below is given in Appendix 1:

Life form shrub, treelet, or small tree to 5 m high (small shrub, not exceeding 4 m in height), multi- or single-stemmed, with short and long side shoots (usually multi-stemmed, principally characterized by the production of short shoots); leaves deciduous (persistent [evergreen]); inflorescences axillary or terminal—axillary and then terminal by the continuation of meristematic activity (inflorescences terminal); inflorescences with three calyculi (inflorescences possessing cataphylls but without calyculi or bracteoles); uppermost calyculus bearing one or rarely two leaf-sized foliar lobes (inflorescences with one to three pairs of leaves); flowers with long corolla tubes (relatively short corolla tubes); anthers more or less sessile (non-sessile) and partially exserted (exserted or semi-exserted).

Leroy (1980a, 1982) stated that the development of *Coffea* subg. *Baracoffea* is sympodial, but we can only confirm that certain aspects of plant architecture follow this type of growth pattern (i.e., the influence of inflorescence development on shoot architecture, see Appendix 1). We concur with Leroy (1980a, 1982) that the flowers of *Coffea* subg. *Baracoffea* possess long styles, and that the fruits are bacciform. We did not test the seeds of *Coffea* subg. *Baracoffea* for caffeine content and so could not investigate Leroy's (1980a) claim that the seeds of this subgenus lack or have negligible amounts of caffeine. The use of caffeine and chlorogenic acids for the systematic study of *Coffea* and *Psilanthus* has been investigated by several workers (e.g., Clifford et al., 1989), although a fully comprehensive study has yet to be undertaken (Stoffelen, 1998).

Charrier (1978) proposed a simplified characterization for *Coffea* subg. *Baracoffea*, using the invalid name "Paracoffea subg. Insulanoparacoffea" (see Table 1). According to Charrier (1978: 111) this group is characterized by six principal characters: (1) monopodial and sympodial growth; (2) shrubby habit; (3) deciduous leaves; (4) terminal one-flowered inflorescences; (5) corolla tube more or less long; and (6) stamens exserted. Our characterization agrees with characters 1, 3, and 5 but not 2, 4, and 6, as outlined above. In *Coffea* subg. *Baracoffea* the leading shoot is mostly monopodial and the side shoots are sympodial (e.g., see Figs. 2 and 3).

Morphological study of *Coffea* and *Psilanthus* (the "core Coffeeae") yielded 24 characters suitable for systematic study. Cladistic analyses were performed on the morphological data using different combinations of taxa within the "core Coffeeae" (species, subgenera, and subgenera and species of uncertain affinity) and choice of characters (all characters vs. selected characters, e.g., see Table 2). Resulting cladograms had little or no resolution and low bootstrap support values, and for this reason are not reported here.

DISCUSSION

Species belonging to *Coffea* subg. *Baracoffea* (excluding *C. rhamnifolia*) possess a unique combination of characters not found in any other group of Rubiaceae (characters 2–12, 15–18, 19, 21, 24; see Table 2 and Appendix 1). The presence of a single foliar lobe on the upper calyculus (character 13) is almost unique for the subgenus, except that the upper calyculus of *C. humbertii* (and sometimes *C. grevei*) has two lobes. The four undescribed species of *Coffea* examined for this study (*C.* sp. nov. 1–4) share the aforementioned character and the unique combination of characters and are thus identified as members of *Coffea* subg. *Baracoffea*, although the flowers of *C.* sp. nov. 2 and 3, and the fruits of *C.* sp. nov. 4 are as yet unknown. Two of the undescribed species, *C.* sp. nov. 1 and 2, have ruminate endosperm (character 23, see Fig. 6C), a character shared with the type species of *Coffea* subg. *Baracoffea* (*C. humbertii*), and possess extra-axillary domatia (see Appendix 1, character 5). These two characters are not found in any other members of the "core Coffeeae."

Of the 24 characters enumerated in this study *Coffea* subg. *Baracoffea* (excluding *C. rhamnifolia*) shares the highest number with *Psilanthus* subg. *Afrocoffea*. These two subgenera have the same shoot architecture and inflorescence morphology (characters 2, 6, 7, 8, 9, 11, 12), and share features of leaf morphology (3, 4) and some aspects of floral morphology (15, 16). A reoccurring feature of our unweighted cladistic analyses was the placement of *Coffea* subg. *Baracoffea* with *Psilanthus* subg. *Afrocoffea*. *Psilanthus* subg. *Afrocoffea* differs from *Coffea* subg. *Baracoffea* in the number of foliar lobes on the upper calyculus (character 13), most aspects of floral morphology (17, 18, 19, 20, 21), and by the mean number of pollen apertures (24). Three characters unite *Coffea* subg. *Coffea* with *Coffea* subg. *Baracoffea* (and *C. rhamnifolia*): anthers submedifixed (character 18), long styles (21), and predominately 3-colporate pollen grains (24, see Appendix 1 for discussion). To summarize: on the basis of floral and pollen morphology *Coffea* subg. *Baracoffea* (excluding *C. rhamnifolia*) appears to be most closely allied to *Coffea* subg. *Coffea*, whereas non-floral (vegetative and inflorescence) morphology infer a relationship with *Psilanthus* subg. *Afrocoffea*.

TABLE 2.

Comparative table of morphological differences between the four subgenera of the 'core Coffeeae' (*Coffea* and *Psilanthus*) and selected OTUs. See Appendix 1 for further discussion of characters.

Explanation of general symbols: feature present/positive: +; absent/negative:– ; more or less: ±; rarely/sometimes: ( )

	Coffea		*Psilanthus*			
Characters	subg. *Coffea*	subg. *Baracoffea*	subg. *Psilanthus*	subg. *Afrocoffea*	*C. rhamnifolia*	*P. melanocarpus*
1. Habit	T, sT	S, sT	sT, ?S	?	S	?
2. Shoot architecture	–	+	–	+	+	–
3. Leaves	E(D)	D	E	D(E)	D	E
4. Leaf blades	± G	P	G	G; P	G	G
5. Domatia	A	A & EA (2 spp.)	A	A	A	A
6. Inflorescence position	A	A > T; T	A	A > T; T	A > T; T	A
7. Inflorescence: number per axil or apex	1 – >7	1	1(–3)	1	1	1–3
8. Inflorescence: number of flowers per inflorescence unit	1 – ∞	1	1	1; 1 sp. 1–2(–3)	1	1
9. Calyculi: basic shape	t or c	o-d	t	o-d	o-d	t
10. Stipular lobes: middle calyculus	stip	s-a, rarely m	stip	s-a, rarely m	± s-a	stip
11. Foliar lobes: middle calyculus	ff	sc	ff	sc	sc	ff
12. Foliar lobes: upper calyculus	sm	eq	sm	eq	eq	sm
13. Foliar lobes: upper calyculus	2	1(–2)	2	2	2	2

14. Calyx: lobes accrescent	–	–	+	–	–	–
15. Corolla tube/lobe length ratio	< L, = L, (±> L)	>> L	>> L	>> L	± = L	>> L
16. Corolla tube: external surface	G	P	P or G	P or G	G	P
17. Filaments: length	L	S	A	A	L	S
18. Anthers/filaments: attachment	sub	sub	supr	supr	sub	sub
19. Anthers: position	E	PE	I	I	E	I
20. Anthers: sterile appendages	–	–	+	+ or –	–	–
21. Style: length	L	L	S	S	L	S
22. Fruit: shape	L>W	L<W, or L>W	L>W	L<W	L>W	L=W
23. Seeds: ruminate endosperm	–	– or +	–	–	–	–
24. Pollen: no. of apertures	± 3	± (2–)3	± 3 or 4	± (3–)4 or 5	± (2–)3	± 3 or 4

Explanation of specific symbols and abbreviations: (1) Habit—tree: T; small tree or treelet: sT; shrub: S. (2) Shoot architecture—architecture not influenced by flowering: – ; architecture influenced by flowering: +. (3) Leaves—evergreen: E; deciduous: D. (4) Leaf blades—glabrous: G; pubescent: P. (5) Domatia—axillary (or absent): A; extra-axillary: EA. (6) Inflorescence position—axillary: A; axillary then terminal: A > T; terminal: T. (7) Inflorescence: number of inflorescence units per axil or apex—numerical value. (8) Inflorescence: number of flowers per inflorescence unit—numerical value. (9) Calyculi: basic shape—tubular: t; cup-like: c; open-divergent: o-d. (10) Stipular lobes: middle calyculus—resembling the stipules: stip; stiff and awn-like: s-a; membranous: m. (11) Foliar lobes: middle calyculus—chartaceous or subcoriaceous, flexible, flat or slightly concave: ff; stiff, concave: sc. (12) Foliar lobes: upper calyculus—small, at most subfoliaceous: sm.; ± identical to the vegetative leaves: eq. (13) Foliar lobes: upper calyculus—numerical value. (14) Calyx: accrescent lobes—presence/absence. (15) Corolla tube/lobe length ratio—tube shorter than lobes: <L; tube the same length as lobes: = L; tube slightly longer than lobes: ±> L; tube much longer than lobes: >> L. (16) Corolla tube: external surface—glabrous: G; pubescent: P. (17) Filaments: length—absent or very short (0–0.5 mm long): A; short (≤ 1 mm long): S; long (≥ 2 mm long): L. (18) Anthers: attachment—submedifixed: sub; supramedifixed: supr. (19) Anthers: position—3/4—fully emergent: E; partly emergent (1/2–2/3): PE; mostly or fully included (0–1/3): I. (20) Anthers: sterile appendages—presence/absence. (21) Style length—long, stigma lobes positioned near or above anthers: L; short, stigma lobes positioned distinctly below anthers: S. (22) Fruit shape: length to width ratio—length ± equals width (spherical or subspherical): L = W; length greater than width (ellipsoid to broadly ellipsoid, or obovoid): L>W; length less than width (usually laterally compressed and didymous): L<W. (23) Seeds: ruminate endosperm—presence/absence. (24) Pollen: number of apertures—numerical value.

On the matter of the systematic position of *C. rhamnifolia*, we cannot convincingly place this species within the "core Coffeeae," although morphology and pollen data (character 24) infer a closer relationship with *Coffea*, rather than *Psilanthus*. *Coffea rhamnifolia* and *Coffea* subg. *Coffea* share all the floral characters identified in this study (characters 15, 16, 17, 18, 19, 20, 21), have glabrous leaves (4), two foliar lobes on the upper calyculus (13), and a similar fruit shape (22). Shoot architecture, deciduousness, and certain aspects of inflorescence morphology (2, 3, 6, 7, 9, 11, 12), on the other hand, link *C. rhamnifolia* with *Coffea* subg. *Baracoffea*, and *Psilanthus* subg. *Afrocoffea*. Weighing-up all the morphological evidence, and given that *C. rhamnifolia* is restricted to Somalia and Kenya, it is more likely that this species shares a closer relationship with *Coffea* subg. *Coffea*—rather than *Coffea* subg. *Baracoffea*. This view contradicts the conclusion made by Leroy (1982), that *C. rhamnifolia* should be placed in *Coffea* subg. *Baracoffea.*

Psilanthus (*Psilanthus* subg. *Psilanthus* and *Psilanthus* subg. *Afrocoffea*, including *P. melanocarpus*) can be separated from *Coffea* (*Coffea* subg. *Coffea*, *Coffea* subg. *Baracoffea* and *C. rhamnifolia*) on the basis of absent or very short filaments (character 17, except for *P. melanocarpus*), supramedifixed anthers (18 except for *P. melanocarpus*), included or just emergent anthers (19), short styles (21), and mean number of pollen apertures (24; after Stoffelen et al., 1997). *Psilanthus* subg. *Afrocoffea* (excluding *P. melanocarpus*) differs from *Psilanthus* subg. *Psilanthus* by its shoot architecture (2), deciduousness (3), inflorescence position (6), calyculi morphology (9, 10, 11, 12), non-accrescent calyx lobes (14), and fruit shape (22).

The systematic position of *Psilanthus melanocarpus* has been the subject of debate (e.g., Leroy, 1980a, 1980b, 1981, 1982; Andreasen & Bremer, 1996) but at the present time is still maintained within *Psilanthus* subg. *Afrocoffea* (e.g., Bridson, 1987; Stoffelen, 1998). Our morphological data do not support a close relationship with *Psilanthus* subg. *Afrocoffea*, however, as *P. melanocarpus* shares more characters with *Psilanthus* subg. *Psilanthus* (2, 3, 6, 9, 10, 11, 12, and possibly 24). *Psilanthus melanocarpus* differs from *Psilanthus* subg. *Psilanthus* by having non-accrescent calyx lobes (14), longer filaments (17), submedifixed anthers (18), and a different fruit shape (22). Within the "core Coffeeae" accrescent calyx lobes are restricted to *Psilanthus* subg. *Psilanthus* (*P. mannii* and *P. sapinii*). Our data infer that *P. melanocarpus* should be removed from *Psilanthus* subg. *Afrocoffea*, but we cannot say where this taxon should be placed within the "core Coffeeae." Andreasen and Bremer (1996) suggested that *P. melanocarpus* should be placed either in a genus of its own or in *Coffea*, rather than be included in *Psilanthus*. Our morphological data, however, do not support the placement of *P. melanocarpus* within *Coffea*.

One of the main reasons for the failure of our study to produce meaningful assessments of relationships using cladistic methods is due to the conflict between vegetative/inflorescence characters (characters 1–14) and floral/fruit characters (15–24). For example, an analysis containing six OTUs (as in Table 2) and more than 20 characters either resulted in trees with zero resolution or trees with very weakly supported relationships. Weighting floral characters (e.g., 15–21) favored the grouping of species (or other selected taxonomic units) into their constituent subgenera and genera, in-line with the current classification of the "core Coffeeae" (except for *C. rhamnifolia,* which was placed within *Coffea*), but this is probably not surprising given that the present taxonomy of this group is based on floral characters (Leroy, 1980b; Bridson, 1987, 1988a, 1988b).

The results of a combined molecular and morphological study for the Ixoroideae by Andreasen and Bremer (2000) are of interest here, even though species of *Coffea* subg. *Baracoffea* were not included in their analyses. Five species of "core Coffeeae" were included in their combined data analysis (*rbc*L and ITS sequences, restriction enzyme analysis, and morphological data; see their fig. 5): *C. arabica*, *C. buxifolia* A. Chev. (determined by Andreasen & Bremer as *Coffea* sp. nov.), *P. mannii*, *P. ebracteolatus* Hiern, and *P. melanocarpus* (given by Andreasen & Bremer as

"Paracoffea melanocarpa"). *Psilanthus melanocarpus* is sister to *P. mannii* and *P. ebracteolatus*, forming a *Psilanthus* clade (jackknife value > 50%: 89; Bremer support value 3). And the two species of *Coffea* are placed together (supported by a jackknife value > 50% of 83; Bremer support value 2), forming a sister group to the *Psilanthus* clade. Their combined analysis, although very provisional, infers that the separation of "core Coffeeae" into two genera (i.e., *Coffea* and *Psilanthus*) based on floral characters (and supported by the mean number of pollen apertures) is justified.

Clearly, more systematic data are needed, not only to resolve the relationships within the "core Coffeeae" but also to ascertain which groups of characters (e.g., floral/fruit or vegetative/inflorescence) support the evolutionary history of the group. Anatomical data from fruit and seeds might provide further systematic characters; Stoffelen (1998), for example, stressed the value of seed coat morphology for systematic studies of *Coffea* and *Psilanthus*. In a wider context, further sampling of taxa (e.g., former members of the Gardenieae–Diplosporinae sensu Robbrecht & Puff, 1986, and Robbrecht, 1988) is required for future systematic studies of the Coffeeae, and in particular the genera *Argocoffeopsis* Lebrun (incl. *Argocoffea* (Pierre ex De Wild.) Lebrun), *Calycosiphonia* Robbr., *Discospermum* Dalzell, *Nostolachma* T. Durand, and *Sericanthe* Robbr.

In our morphological reassessment of *Coffea* subg. *Baracoffea* we have shown that the Malagasy representatives of this subgenus form a convincing monophyletic group. *Coffea* subg. *Baracoffea* is separated from other members of the "core Coffeeae" by a unique combination of characters and one nearly discrete character. We were not able to convincingly elucidate the systematic position of *Coffea* subg. *Baracoffea* using morphological data. Likewise, *C. rhamnifolia* and *P. melanocarpus* remain taxa of uncertain taxonomic position, although our data infer that *C. rhamnifolia* is more likely to be a member of *Coffea* subg. *Coffea*, rather than *Coffea* subg. *Baracoffea* (see Davis, 2003). Given the number of morphological differences between the two subgenera of *Coffea* it could be argued that *Coffea* subg. *Baracoffea* should be raised to the rank of genus. It is quite obvious, however, that additional systematic data are required before any taxonomic decisions can be made. In particular, it is necessary to clarify the placement of *C. rhamnifolia*, as it is the type of the genus *Paolia* Chiov.

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APPENDIX 1. CHARACTERS.

The characters discussed below are summarized in Table 2. Discussion of characters for *Coffea* subg. *Baracoffea* include *C. rhamnifolia* unless otherwise stated.

1. HABIT

Species of ***Coffea*** subg. ***Baracoffea*** are either multi-stemmed shrubs (e.g., ***C. grevei, C. humbertii***), or small trees (e.g., ***C. decaryana***, and ***C***. spp. nov. 1, 2, and 3). We have observed that at least one species can develop from a multi-stemmed shrub into a small single-stemmed tree: ***C. grevei***, which is normally a multi-stemmed shrub 1–2 m high, becomes a small single-stemmed tree with age (ca. 20 years), reaching 5 m high with a diameter at breast height (dbh) of 5 cm. All species of ***Coffea*** subg. ***Coffea*** exist as treelets, small trees, or trees (e.g., ca. 10 m high), i.e., they are single-stemmed plants. Specimens of ***Coffea*** subg. ***Coffea*** are quite often described as shrubs on herbarium specimen labels, yet field observations in Africa (A. Davis, pers. obs.) and Madagascar (A. Davis & F. Rakotonasolo, pers. obs.) show that they have a single trunk (i.e., treelets, small trees, or trees). We have not had the opportunity to determine the life form of many ***Psilanthus*** species, as this requires the examination of plants in situ, but can state that ***P. ebracteolatus*** vel aff. and ***P. mannii*** are treelets. Detailed field observations are required to fully characterize the architecture of ***Coffea*** and ***Psilanthus***.

2. SHOOT ARCHITECTURE

The inflorescences of ***Coffea*** subg. ***Baracoffea*** and most ***Psilanthus*** subg. ***Afrocoffea*** are indeterminate, and have a direct influence on the architecture of the plant. That is, after flowering or fruiting the development of the inflorescence continues, either by the production of inflorescences or the growth of a vegetative shoot. Development of the inflorescence continues by one, or sometimes two, lateral (relay) axes, each of which produces either an inflorescence or a vegetative shoot during the following growth season (see Figs. 1A, 1B, 1D, 2B). Sometimes an inflorescence can be produced on a long vegetative side shoot, although observations over a several-year period would be necessary to determine whether the vegetative shoot had originated as an inflorescence. In ***Coffea*** subg. ***Coffea***, ***Psilanthus*** subg. ***Psilanthus***, and ***Psilanthus melanocarpus*** (***Psilanthus*** subg. ***Afrocoffea***) the inflorescences are determinate: after flowering or fruiting the inflorescence does not continue growth (see Figs. 1C, 2A). The apical meristem of the indeterminate shoot continues its vegetative activity while producing determinate axillary inflorescences; in most species long plagiotrophic branches are produced.

3. LEAVES (DECIDUOUS OR EVERGREEN)

The leaves of all species of ***Coffea*** subg. ***Baracoffea*** (and ***C. rhamnifolia***) are deciduous, as are most ***Psilanthus*** subg. ***Afrocoffea***. The leaves of ***Psilanthus*** subg. ***Psilanthus***, ***P. melanocarpus*** (***Psilanthus*** subg. ***Afrocoffea***), and most ***Coffea*** subg. ***Coffea***, are evergreen. Only three species of ***Coffea*** subg. ***Coffea*** have deciduous leaves, namely ***C. zanguebariae***, ***C. racemosa***, and ***C***. sp. J (of Bridson, 1982). The flowers of ***Coffea*** subg. ***Baracoffea***, and most species of ***Psilanthus*** subg.

Afrocoffea are produced on leafless shoots (e.g., see Fig. 3A), or on shoots with recently produced developing leaves. Some species of ***Psilanthus*** subg. ***Afrocoffea*** (e.g., ***P. semsei*** Bridson) can produce flowers when the leaves are more or less fully developed (see Fig. 1A).

In the "core Coffeeae" deciduousness may have evolved in response to seasonally dry habitats as there is a correlation between environment and seasonal leaf fall. For example, all species of ***Coffea*** subg. ***Baracoffea*** (except ***C. rhamnifolia***) occur in the seasonally dry, deciduous forests of western Madagascar; ***C. rhamnifolia*** is found in the drylands of northeastern Africa; and the three deciduous species of ***Coffea*** subg. ***Coffea*** occur in seasonally dry regions of tropical southeastern Africa and South Africa. In contrast, most evergreen species of ***Coffea*** subg. ***Coffea*** are found in humid, evergreen forest. This correlation is by no means absolute, however, as evergreen species of ***Coffea*** subg. ***Coffea*** sometimes occur in deciduous forest. In Madagascar, for example, evergreen species of ***Coffea*** subg. ***Coffea*** (e.g., ***C. boiviniana*** (Baill.) A. Chev. and ***C. moratii*** A. P. Davis & Rakotonas. (see Davis & Rakotonasolo, 2003) are found with deciduous ***Coffea*** subg. ***Baracoffea***.

4. LEAVES (PUBESCENT OR GLABROUS)

All species of ***Coffea*** subg. ***Baracoffea*** have pubescent leaves, apart from ***C. rhamnifolia***. In ***C. decaryana*** the margins, adaxial leaf surface, midrib, and veins are moderately to densely covered with hairs. The other species possess hairs mainly on the midrib and major veins of the abaxial leaf surface. The leaves of ***Coffea*** subg. ***Coffea*** are glabrous, although several species have leaves that are sometimes sparsely and minutely puberulous on the veins on the abaxial surface, and particularly the midrib (e.g., ***C. brevipes*** Hiern, ***C. canephora***, ***C. congensis*** A. Froehner, ***C. humilis*** A. Chev., ***C. magnistipula*** Stoff. & Robbr.). The leaves of ***Psilanthus*** subg. ***Psilanthus*** are more or less glabrous; sometimes the veins on the abaxial surface are sparsely puberulous. The leaves of ***Psilanthus*** subg. ***Afrocoffea*** can be glabrous or pubescent (hairs confined to the midrib and major venation).

5. LEAVES (DOMATIA)

Many species in the "core Coffeeae," including all species of ***Coffea*** subg. ***Baracoffea***, possess domatia. The domatia are located on the adaxial surface of the leaf, usually against or near the midrib (primary vein) where the midrib connects with the bases of the secondary veins, and quite often they are positioned in the axil where the midrib and secondary veins meet. Two undescribed species of ***Coffea*** subg. ***Baracoffea***, ***C.*** spp. nov. 1 and 2, are the only members of the "core Coffeeae" that have domatia located at the branching points of the secondary and tertiary veins (here termed as "extra-axillary domatia"). Sometimes the domatia are paired, one on either side of a secondary vein. Depending on the length of the secondary vein, there are one to four extra-axillary domatia per secondary vein.

6. INFLORESCENCE POSITION

The inflorescences of ***Coffea*** subg. ***Baracoffea*** are either axillary (in the leaf axils of indeterminate shoots, see Figs. 2B, 3A) or terminal (at the apices of short determinate shoots, see Figs. 1D, 2B, 3A). Axillary inflorescences are converted into terminal inflorescences by renewed seasonal meristematic activity (see 2. ***Shoot architecture***, and Fig. 2B). After several flowering seasons the original axillary inflorescence usually becomes a brachyblast (a short condensed shoot), either bearing an inflorescence (see Figs. 1D, 3A) or leaves (i.e., becoming vegetative). The terminal inflorescences either occur on a shoot that has previously not borne flowers (although it is not certain whether the shoot originated as an inflorescence) or on a brachyblast that has previously borne only inflorescences (see 2. ***Shoot architecture***). The inflorescence position and architecture of the flowering shoot in ***Psilanthus*** subg. ***Afrocoffea*** follows the same basic pattern as ***Coffea*** subg. ***Baracoffea***.

The inflorescence position of ***Coffea*** subg. ***Coffea***, ***Psilanthus*** subg. ***Psilanthus***, and ***P. melanocarpus*** (***Psilanthus*** subg. ***Afrocoffea***) is strictly axillary.

Characters 7–13: Notes on inflorescence structure with particular reference to calyculi

All "core Coffeeae" have the same basic inflorescence structure, that is, they possess calyculi (Robbrecht, 1978: 18; Stoffelen, 1998: 59). In all species of ***Psilanthus***, ***Coffea*** subg. ***Baracoffea***, and many species of ***Coffea*** subg. ***Coffea*** the ***basic inflorescence unit*** has three calyculi (see Figs. 4A, 4E, 5A, 5B), but occasionally there may be only two, or four or more calyculi. Some species of ***Psilanthus*** subg. ***Afrocoffea*** (e.g., ***P. ebracteolatus, P. bengalensis*** (Schult.) J.-F. Leroy) and ***Coffea*** subg. ***Baracoffea*** (i.e., ***C. humbertii***, ***C. grevei***, and ***C.*** sp. nov. 3) infrequently produce flowers that apparently lack calyculi. In most of these cases, however, the calyculi are actually present but have become separated by shoot-growth between the calyculi. This is particularly noticeable in specimens of ***P. bengalensis***, and may be due to environmental influence (e.g., high rainfall). Infrequently, the inflorescence is represented by a single flower at the apex of a short shoot bearing two or three pairs of normal shoot leaves (e.g., ***P. ebracteolatus***). Stoffelen (1998) reported that calyculi ("bracteal cups") are absent in ***P. ebracteolatus,*** but we conclude that this species usually possesses three calyculi. Several species of ***Coffea*** subg. ***Coffea*** have numerous calyculi in each inflorescence (e.g., 12 or more). In these cases the inflorescences are compound and consist of multiple basic inflorescence units.
Each calyculus is undoubtedly formed from reduced leaves and stipules (Davis & Rakotonasolo, 2000: 405), which are fused together (to varying degrees) to form a structure often resembling a four-lobed tubular (or cup-like) calyx limb. Each calyculus has two pairs of lobes, the foliar lobes and the stipular lobes, which are derived from leaves and stipules, respectively. It is possible to deduce the origin of each lobe (i.e., stipule or leaf) even when they are highly reduced.

As most members of the "core Coffeeae" have three calyculi it is usually possible to name and number each calyculus. This often allows comparisons to be made between taxa. For the purposes of this study we have followed the convention used by Davis and Rakotonasolo (2000, 2001); the calyculi are numbered starting from the base of the inflorescence (i.e., from leaf axil or apex of shoot) upward (see Fig. 5): the lower calyculus (1st), the middle calyculus (2nd), and the upper calyculus (3rd). Where the number of calyculi is uncertain, this numbering sequence may also be invoked from the flower downward, so that the upper calyculus (3rd) is immediately below the flower, the middle (2nd) below the upper (3rd), and the lower (1st) below the middle (2nd). In ***Coffea*** subg. ***Coffea*** the lower (1st) calyculus often falls in the early stages of inflorescence development.

In several species of **Coffea** subg. **Coffea** (e.g., **C. sessiliflora** Bridson, **C. littoralis** A. P. Davis & Rakotonas., and **C. ratsimamangae** J.-F. Leroy ex A. P. Davis & Rakotonas., see Fig. 4A) free bractlets are present on the pedicel. This feature does not seem to be of any considerable systematic consequence, although the fact that pedicel bractlets are not present in **Coffea** subg. **Baracoffea**, and have not been recorded in **Psilanthus**, should not be overlooked.

7. INFLORESCENCE (NUMBER OF INFLORESCENCES PER LEAF AXIL OR SHOOT APEX)

All species of **Coffea** subg. **Baracoffea** and all **Psilanthus** (except **P. melanocarpus**) have one inflorescence per axil or apex (e.g., Figs. 1A, 1B, 1C, 3A). In **Coffea** subg. **Coffea** there can be one to several inflorescences per axil, but usually there are two to three (e.g., see Fig. 6G). In **P. melanocarpus** there are one to three inflorescences per axil; **P. mannii** (**Psilanthus** subg. **Psilanthus**) has one per axil, or rarely up to three.

8. NUMBER OF FLOWERS PER INFLORESCENCE

All species of **Coffea** subg. **Baracoffea** and **Psilanthus** subg. **Afrocoffea** (excluding **P. ebracteolatus**) have one flower per inflorescence. **Psilanthus ebracteolatus** has one to three flowers per inflorescence. Some species of **Coffea** subg. **Coffea** have one flower per inflorescence, but many species have inflorescences with two or more flowers (e.g., up to 10 in **C. dubardii** Jum. and up to 30 or more in some **C. arabica** cultivars). **Psilanthus** subg. **Psilanthus** and **P. melanocarpus** have one flower per inflorescence unit.

9. CALYCULUS SHAPE

The calyculi of **Coffea** subg. **Baracoffea**, and most **Psilanthus** subg. **Afrocoffea**, are loose open structures. The calyculi parts are adnate near the base, and the foliar lobes are divergent (especially in **Coffea** subg. **Baracoffea**, see Figs. 3C, 4E, 5B). The lower calyculus of **Coffea** subg. **Baracoffea** can be almost cup-like, but the foliar lobes are divergent and spreading. In **Coffea** subg. **Coffea** (e.g., see Figs. 4A, 5A, 6G), **Psilanthus** subg. **Psilanthus**, and some species of **Psilanthus** subg. **Afrocoffea** (**P. melanocarpus**, **P. leroyi** Bridson, **P. malabaricus** Sivar., Biju & P. Mathew, and **P. lebrunianus** (R. Germ. & Kesler) J.-F. Leroy ex Bridson) the calyculi are more or less tubular; the foliar and stipular lobes of each calyculus are adnate for most of their length. Some species of **Coffea** subg. **Coffea** (e.g., **C. canephora** and **C. manombensis** A. P. Davis) produce subfoliaceous foliar lobes but the calyculi remain tube-like, indicating that the overall shape of the calyculi is not influenced by the size of the foliar lobes.

10. MIDDLE (2ND) CALYCULUS (STIPULAR LOBES)

Most **Coffea** subg. **Baracoffea** and **Psilanthus** subg. **Afrocoffea** possess a middle calyculus with stiff, narrowly triangular stipular lobes ("cataphylls" of Leroy, 1980a, 1982; or "scarious bracts" of Bridson, 1982) (e.g., see Fig. 4E). In most cases they are larger than the stipules of the regular vegetative shoot. In some taxa this type of stipular lobe is also found on the lower calyculus (e.g., **P. semsei**). The stipular lobes of **Coffea** subg. **Coffea** and **Psilanthus** subg. **Psilanthus** resemble the stipules (of the vegetative shoot) and are never stiff and awn-like.

11. MIDDLE (2ND) CALYCULUS (FOLIAR LOBES)

In **Coffea** subg. **Baracoffea** and **Psilanthus** subg. **Afrocoffea** the foliar lobes of the middle calyculus are stiff and distinctly concave (e.g., see Figs. 3C, 4E), and often fall during the early stages of flower development. The same structures in **Coffea** subg. **Coffea** and **Psilanthus** subg. **Psilanthus** are either chartaceous or subcoriaceous, flexible, and flat or only slightly concave.

12. UPPER (3RD) CALYCULUS (FOLIAR LOBES)

Coffea subg. **Baracoffea** and **Psilanthus** subg. **Afrocoffea** (excluding **P. melanocarpus** and **P. malabaricus**) are the only subgenera of the "core Coffeeae" that have foliar lobes equal in size and morphology to the shoot leaves (see Figs. 1D, 6D) when fully developed. In **Coffea** subg. **Coffea**, **Psilanthus** subg. **Psilanthus**, and **P. melanocarpus,** the foliar lobes are greatly reduced (e.g., see Fig. 6G), shortly lobed (e.g., see Fig. 4A), or at the most subfoliaceous (e.g., **C. canephora**).

13. UPPER (3RD) CALYCULUS (NUMBER OF FOLIAR LOBES)

Coffea subg. **Baracoffea** is the only subgenus of the "core Coffeeae" to have a single leaf-like foliar lobe on the upper (or any other) calyculus (e.g., see Figs. 1D, 6D). **Coffea humbertii** is the only exception, with two leaf-like foliar lobes, although occasionally **C. grevei** can also have two lobes. The presence of a single leaf-like foliar lobe makes the inflorescence appear leaf-opposed, an obvious feature when the members of this subgenus are observed in fruit (see Fig. 6D). Field studies of **Coffea** subg. **Baracoffea** (i.e., **C.** sp. nov. 1) show that a small subfoliaceous foliar lobe (ca. 2–3 mm long) is sometimes present, opposite the leaf-like foliar lobe (ca. 8 cm long). The smaller lobe either falls early in flower development or persists until the early stages of fruit development. When the vestigial subfoliaceous lobe is absent (fallen), examination at flower bud stage shows that there is a short collar of tissue and a small number of colleters where a foliar lobe would otherwise have been attached (see Fig. 3C). As development of the flower continues this collar becomes invisible but the colleters usually remain. It seems, then, that the single leaf-like foliar lobe of the upper calyculus has been derived by the reduction and then loss of one of the foliar lobes (in each pair).

14. CALYX LOBES

In **Psilanthus** subg. **Psilanthus** calyx lobes are present and distinctly accrescent: at flowering time the calyx lobes are usually less than 3 mm long but develop significantly during fruit development to over 20 mm long. In **Psilanthus** subg. **Afrocoffea** the calyx lobes are small and often irregular but never accrescent. The calyx of **Coffea** subg. **Coffea** and **Coffea** subg. **Baracoffea** is usually truncate to undulate, or weakly lobed and non-accrescent.

15. COROLLA TUBE (LENGTH)

The length of the corolla tube has been used as a distinguishing character in identification keys for the "core Coffeeae" (e.g., Bridson, 1988a; Stoffelen, 1998: 33). According to Bridson's key, in **Coffea** subg. **Coffea** and **C. rhamnifolia** the corolla tube and lobes are subequal, while in **Coffea** subg. **Baracoffea** the corolla tube is longer than the lobes. While this is true for most species of **Coffea** subg. **Coffea**, some of the more recently described taxa (after 1994) have a corolla tube much shorter than the lobes (e.g.,

C. montekupensis Stoff., ***C. lulandoensis*** Bridson), and in some species the tube is longer than the lobes (e.g., ***C. heterocalyx*** Stoff., and ***C. dubardii***). However, in ***Coffea*** subg. ***Baracoffea*** and ***Psilanthus*** the corolla tube is usually at least three times longer than the lobes. In this respect, ***C. rhamnifolia*** differs from all other members of ***Coffea*** subg. ***Baracoffea***, because the corolla tube is roughly the same length as the lobes (as in most ***Coffea*** subg. ***Coffea***). The corolla tube of ***P. mannii*** (***Psilanthus*** subg. ***Psilanthus***) is markedly longer than all other members of the "core Coffeeae" (up to 70 mm long).

16. COROLLA (PUBESCENT OR GLABROUS)

In all species of ***Coffea*** subg. ***Baracoffea*** (except ***C. rhamnifolia***), many species of ***Psilanthus*** subg. ***Afrocoffea*** (e.g., ***P. bengalensis***, ***P. fragrans*** (Wall. ex Hook.f.) J.-F. Leroy, ***P. wightianus*** (Wall. ex Wight & Arn.) J.-F. Leroy, ***P. semsei***, ***P. leroyi***, ***P. melanocarpus***) the external surface of the corolla tube is sparsely pubescent to pubescent. All species of ***Coffea*** subg. ***Coffea*** and some ***Psilanthus*** subg. ***Afrocoffea*** (e.g., ***P. travancorensis*** (Wight & Arn.) J.-F. Leroy, ***P. ebracteolatus***, ***P. lebrunianus***) are glabrous. In the corolla of ***P. mannii*** (***Psilanthus*** subg. ***Psilanthus***) it is either glabrous or sparsely pubescent.

17. FILAMENT LENGTH

The filaments of ***Coffea*** subg. ***Baracoffea*** and ***P. melanocarpus*** (***Psilanthus*** subg. ***Afrocoffea***) are very short (ca. 1 mm long); the anthers move when touched but they are not versatile. In ***Coffea*** subg. ***Coffea*** and ***C. rhamnifolia*** (***Coffea*** subg. ***Baracoffea***) the filaments are relatively long (ca. 2 mm or more) and the anthers are versatile. In ***Psilanthus*** subg. ***Psilanthus*** and ***Psilanthus*** subg. ***Afrocoffea*** (excluding ***P. melanocarpus***) the filaments are very short or more or less absent and the anthers are non-versatile. Examination of the anthers at low magnification (× 20) shows that there is either a small piece of tissue at the back of the anthers, where they are attached to the corolla (e.g., ***P. semsei***), or the anthers appear to be attached directly to the corolla. Micromorphological studies are required to ascertain exactly how the anthers are fixed to the corolla tube.

18. FILAMENTS (ATTACHMENT)

In ***Coffea*** subg. ***Coffea***, ***Coffea*** subg. ***Baracoffea***, and ***P. melanocarpus***, the filaments are attached below the mid-point of the anthers (submedifixed; see Fig. 3G). In ***Psilanthus*** subg. ***Psilanthus*** and ***Psilanthus*** subg. ***Afrocoffea*** (but not ***P. melanocarpus***) the attachment is either above the middle point of the anther or close to the apex (supramedifixed). In ***P. semsei***, for example, the point of attachment is close to the tip of the anther (Fig. 4G).

19. ANTHER POSITION AND ORIENTATION AT ANTHESIS

Coffea subg. ***Coffea*** and ***C. rhamnifolia*** (***Coffea*** subg. ***Baracoffea***) are the only members of the "core Coffeeae" to have fully emergent anthers, although they can also be 2/3 emergent before the filaments reflex at anthesis. The anthers are held more or less vertically in bud and when the flowers first open but as the flower matures the filaments reflex and are held either at approximately 30° (to the vertical) to more or less horizontal. The anthers of ***Coffea*** subg. ***Baracoffea*** are 1/2 to nearly 2/3 emergent but are never fully emergent (e.g., see Figs. 3E, 4F). In ***Psilanthus*** subg. ***Psilanthus*** and ***Psilanthus*** subg. ***Afrocoffea*** the anthers are fully included to 1/3 exserted. The position of the anthers in the corolla tube is due to both the position of filament attachment (i.e., submedifixed or supramedifixed, see ***18. Filaments (attachment)***) and the point of attachment of the filaments (or anthers) within the corolla tube. The anthers of ***Coffea*** subg. ***Coffea*** and ***Coffea*** subg. ***Baracoffea*** are attached immediately below the corolla lobes at the top of the corolla tube; those of ***Psilanthus*** subg. ***Psilanthus*** and most ***Psilanthus*** subg. ***Afrocoffea*** are attached slightly lower down the corolla tube.

20. ANTHER APPENDAGES

Most ***Psilanthus*** species possess sterile appendages at the apex of the filaments (see Fig. 4G; Bridson, 1982, fig. 13e). The appendages are usually quite short (e.g., ca. 1 mm long, or less), and either pointed or obtuse at the apex. Of the species examined only ***P. leroyi, P. melanocarpus***, and ***P. travancorensis*** (three species belonging to ***Psilanthus*** subg. ***Afrocoffea***) have anthers lacking sterile appendages. We have not found anther appendages in any species of ***Coffea*** subg. ***Coffea*** or ***Coffea*** subg. ***Baracoffea***.

21. STYLE (LENGTH—EXSERTED OR INCLUDED)

Coffea subg. ***Baracoffea*** and ***Coffea*** subg. ***Coffea*** have long, excluded styles; the stigmatic lobes are positioned roughly equal to, or above, the anthers (e.g., see Fig. 4B, D, F). All species of ***Psilanthus*** have short, included styles; the stigma lobes are positioned well below the anthers (e.g., see Fig. 4H). The character "styles exserted/included" has been used to distinguish ***Coffea*** from ***Psilanthus*** in identification keys (e.g., Bridson, 1988a; Stoffelen, 1998: 33): ***Coffea*** has exserted styles, and ***Psilanthus*** has short included styles.

22. FRUIT SHAPE

Psilanthus subg. ***Afrocoffea*** and most species of ***Coffea*** subg. ***Baracoffea*** have fruits with a greater width to height ratio and are laterally compressed. When viewed from the side they are transversely elliptic and didymous in outline (see Fig. 6E). ***Coffea humbertii***, ***C.*** spp. nov. 1 and 2 (all ***Coffea*** subg. ***Baracoffea***) have more or less obovoid to pyriform fruits (e.g., Fig. 6A). The fruits of ***Coffea*** subg. ***Coffea*** are usually ellipsoid to very broadly ellipsoid, or less often obovoid. They usually have a greater length to width ratio (Fig. 6G), although sometimes it is possible to have spherical monospermic fruits (e.g., the "pea berry" fruits of ***C. arabica*** cultivars; not included in Table 2). The fruits of ***C. rhamnifolia*** (***Coffea*** subg. ***Baracoffea***) are ellipsoid to obovoid, and thus similar to ***Coffea*** subg. ***Coffea***. The fruits of ***Psilanthus*** subg. ***Psilanthus*** are more or less ellipsoid to obconical, longer than wide at maturity, and have very long (e.g., more than 2 cm) accrescent and decurrent calyx lobes, which give the fruit a slightly winged or ribbed appearance. ***Psilanthus melanocarpus*** (***Psilanthus*** subg. ***Afrocoffea***) has more or less spherical fruits.

One species of ***Coffea*** subg. ***Baracoffea***, ***C***. sp. nov. 3, has conspicuously winged fruits (Fig. 6F), which is a character unique within the Coffeeae. These wings are independent of the vascular tracts of the calyx lobes and are thus not analogous with the winged or ribbed fruits of ***P. mannii***. A few species of ***Coffea*** subg. ***Coffea*** (e.g., ***C. kapakata*** (A. Chev.) Bridson) have slightly ribbed fruits, but these are not comparable with those of ***C***. sp. nov. 3. If the wings of ***C***. sp. nov. 3 are removed the shape of the fruit is broader than high, and didymous (e.g., like ***C. grevei*** and ***C. decaryana***).

The mature fruits of *Coffea* subg. *Baracoffea* are either red or green-red (e.g., *C. grevei*) or yellow to yellow flushed with red (e.g., *C.* spp. nov. 1 and 2). The external surface of the fruit can be glabrous or hairy (e.g., see Fig. 6D, E).

23. SEED (ENDOSPERM)

Three species of *Coffea* subg. *Baracoffea* have seeds with ruminate endosperm, a feature absent in all other members of the "core Coffeeae." *Coffea* spp. nov. 1 and 2 have seeds with ruminate endosperm, and *C. humbertii* has weakly ruminate endosperm. The endosperm of *C*. spp. 1 and 2 has shallow invaginations on the external surfaces, particularly on the ventral surface (see Fig. 6C), and the main ventral invagination (i.e., the groove in a "coffee bean") has short second-order invaginations (see Fig. 6B, C). The endosperm of *C. humbertii* is similar to *C*. spp. 1 and 2 except that the invaginations are fewer and not as deep.

24. POLLEN (NUMBER OF APERTURES)

There have been several taxonomic surveys of *Coffea* and *Psilanthus* pollen, the most recent and noteworthy being those of Lobreau-Callen and Leroy (1980), Chinnappa and Warner (1981), and Stoffelen et al. (1997). These studies show that there is a high degree of pollen polymorphism in *Coffea* and *Psilanthus*, specifically in the size of the grains, number, shape, and/or position of the apertures, and texture of the tectum. The pollen polymorphism observed in *Coffea* is greater than that of *Psilanthus*, with variability within an individual and even within one anther (Stoffelen et al., 1997). Despite the significant polymorphism it is possible to summarize that the grains of *Coffea* subg. *Coffea* and *Coffea* subg. *Baracoffea* are generally 3-colporate, and most *Psilanthus* have 4- to 5-colporate grains; *P. mannii* (*Psilanthus* subg. *Psilanthus*) and *P. melanocarpus* (*Psilanthus* subg. *Afrocoffea*) have 3- to 4-colporate grains (Stoffelen et al., 1997). *Coffea humbertii* and *C. grevei* (*Coffea* subg. *Baracoffea*) have 3-colporate grains (Lobreau-Callen & Leroy, 1980); *C. rhamnifolia*, the African representative of this subgenus, has 3-colporate, or rarely 2-colporate grains (Stoffelen et al., 1997). For our study we sampled one of the undescribed species of *Coffea* subg. *Baracoffea* (*C.* sp. nov. 1; *Rakotonasolo 240*) and found that it possessed 3-colporate or sometimes 2-colporate pollen grains. The 2-colporate grains are produced via the loss of a colpus, i.e., the two colpi are in more or less the same position as those of 3-colporate grains. Lack of suitable flowering material prevented us sampling further species of *Coffea* subg. *Baracoffea*.

APPENDIX 2. REPRESENTATIVE MATERIAL EXAMINED.

Coffea subg. **Coffea**

C. arabica L.: ETHIOPIA. *Meyer 8953* (K), *Mooney 8651* (K). SUDAN. *Thomas 3770* (K). **C. brevipes** Hiern: CAMEROON. *Etuge 1168* (K), *Thomas & Nemba 5204a* (K). **C. buxifolia** A. Chev.: MADAGASCAR. *Baron 3152* (K), *Davis 1024* (K, P, MO, TAN), *Pettersson & Nilsson 765* (K). **C. canephora** A. Froehner: UGANDA. *Wood 176* (K), *Greenway & Eggeling 7052* (K). TANZANIA. *Doughty 20* (K). **C. congensis** A. Froehner: CENTRAL AFRICAN REPUBLIC. *Chevalier 5276* (K), *Thomas & Fay 7277* (K). **C. costatifructa** Bridson: TANZANIA. *Greenway 5366* (K), *Ludanga in MRC 1169* (EA), *Vollesen in MRC 4344* (K). **C. dubardii** Jum.: MADAGASCAR. *Davis & Rakotonasolo 2232* (BR, K, MO, P, TAN), *McPherson 14526* (MO, P, TAN), *Capuron 20064-SF* (K, P). **C. heterocalyx** Stoff.: CAMEROON. *de Wilde 3725* (K). CULTIVATED. *Zadi Koubi 410* (K). **C. homollei** J.-F. Leroy: MADAGASCAR. *Capuron 8596-SF* (K, P), *Cours 2591* (K, P), *Manohiraza 102* (P). **C. humblotiana** Baill.: COMOROS. *Humblot 412* (P), *Humblot s.n.* (P), *s. c. 16579-SF* (P). **C. humilis** A. Chev.: LIBERIA. *Adam 20380* (K), *Baldwin 9327* (K), *Harley 1523* (K). **C. kapakata** (A. Chev.) Bridson: ANGOLA. *Gossweiler 9896* (K), *9958* (K). **C. lancifolia** A. Chev. subsp. **auriculata** J.-F. Leroy: MADAGASCAR. *Davis & Rakotonasolo 2310* [*Kianjavato Coffee Research Station acc. no. A. 320*] (K, TAN), *s. c. 14640-SF* (P), *Leroy 215* [*A. 320*] (P). **C. leroyi** A. P. Davis: MADAGASCAR. *Cours 2209* (K, P), *Cours 2639* (K, P), *Herb. Jard. Bot. de Tan. 4358 d* (P). **C. littoralis** A. P. Davis & Rakotonas.: MADAGASCAR. *Capuron 27432-SF* (K, P, TAN). **C. lulandoensis** Bridson: TANZANIA. *Bidgood et al. 732*, *Lovett & Congdon 2032* (K), *Mwangoka et al. 12* (K). **C. magnistipula** Stoff. & Robbr.: GABON. *Breteler et al. 8153* (K). **C. manombensis** A. P. Davis: MADAGASCAR. *Davis & Rakotonasolo 2141* (K, MO, P, TAN, TEF), *Davis & Rakotonasolo 2143* (K, MO, P, TAN). **C. minutiflora** A. P. Davis & Rakotonas.: MADAGASCAR. *Capuron 23553-SF* (BR, K, MO, P, TAN, TEF). **C. montekupensis** Stoff.: CAMEROON. *Cable 1134* (K), *Cheek 7190* (K), *Lane 156* (K). **C. pseudozanguebarieae** Bridson: KENYA. *Kibuwa 1225* (K), *Robertson 232* (K), *3877* (K). **C. racemosa** Lour.: MOZAMBIQUE. *Barbosa & de Lemos 8062* (K), *Leach & Bayliss 11909* (K), *White 6* (K). **C. ratsimamangae** J.-F. Leroy ex A. P. Davis & Rakotonas.: MADAGASCAR. *Capuron 23171-SF* (K, P, TEF). **C. sakarahae** J.-F. Leroy: MADAGASCAR. *Davis & Rakotonasolo 2167* (K, P, MO, TAN), *Capuron 23533bis-SF* (K, P); *Capuron 22199-SF* (K, P). **C. salvatrix** Swynn. & Philipson: TANZANIA. *Stolz 1966* (K). **C. sessiliflora** Bridson subsp. **sessiliflora**: KENYA. *Magogo & Glover 209* (K), *Rawlins 216* (K). **C. sp. J** (of Bridson, 1982): MALAWI. *Brummitt 8936* (K). **C. zanguebariae** Lour.: MOZAMBIQUE. *Forbes s.n.* (K). TANZANIA. *Vollesen in MRC 2982* (K), *3023* (K).

Coffea subg. **Baracoffea**

C. decaryana J.-F. Leroy: MADAGASCAR. *Decary 15842* (P), *Davis & Rakotonasolo 2528* (BR, K, MO, P, TAN, TEF), *Davis & Rakotonasolo APD 2537* (BR, K, MO, P, TAN, TEF). **C. grevei** Drake ex A. Chev. (syn. *C. capuronii* J.-F. Leroy, *C. morondavensis* J.-F. Leroy): MADAGASCAR. *Capuron 22135-SF* (P), *Jongkind & Andriantiana 3746* (K, P, TAN, WAG), *Davis & Rakotonasolo 2561* (K, MO, P, TAN, TEF). **C. humbertii** J.-F. Leroy: MADAGASCAR. *Capuron 20717-SF* (P), *Capuron 20689-SF* (P), *Humbert 20155* (P). **C. rhamnifolia** (Chiov.) Bridson: SOMALIA. *Beckett & White 1527* (K), *Gillett & Hemming 24523* (K), *Thulin & Warfa 5277* (K). **C. sp. nov. 1**: MADAGASCAR. *Rakotonasolo RNF 68* (K, TAN, TEF), *Davis & Rakotonasolo 2553* (BR, K, MO, P, TAN, TEF), *Rakotonasolo RNF 240* (K, TAN, TEF). **C. sp. nov. 2**: MADAGASCAR. *Rakotonasolo RNF 67* (K, TAN, TEF), *Rakotonasolo RNF 122* (K, TAN, TEF), *Davis & Rakotonasolo 2502* (K, MO, P, TAN, TEF). **C. sp. nov. 3**: MADAGASCAR. *Labat & Deroin 2291* (K, P, TAN), *Davis & Rakotonasolo 2538* (K, MO, P, TAN, TEF), *Davis & Rakotonasolo 2519* (K, MO, P, TAN, TEF). **C. sp. nov. 4**: MADAGASCAR. *Bisset M 13* (K).

Psilanthus subg. **Psilanthus**

P. mannii Hook.f.: GHANA. *Hall* 2952 (K), *Harder et al. 3316* (K), *Irvine* 1152 (K). CAMEROON. *Davis et al. 3061* (K), *Sonké 1091* (K), *Thomas 6819* (K), *Thompson 1805* (K).

Psilanthus subg. **Afrocoffea**

P. bababudanii Sivar., Biju & P. Mathew: INDIA. *Browne 5318* (K), *Sivarajan & Biju 20121* (K), *Biju 44701* (K). **P. bengalensis** (Schult.) J.-F. Leroy: INDIA. *Clarke 26392B* (K), *Gamble 979* (K), *Haselfoot Haines 2689* (K). **P. brassii** (J.-F. Leroy) A. P. Davis: NEW GUINEA. *Pullen 6814* (K), *Frodin UPNG 4323* (K). AUSTRALIA. *s. c.* (K). **P. bridsoniae** Sivar., Biju & P. Mathew: INDIA. *Biju & Sasi 44800* (K), *Wight s.n.* (K), *Gamble 14899* (K). **P. ebracteolatus** Hiern: SIERRA LEONE. *Deighton 4724* (K), *Katta 2* (K), *Morton & Gledhill 1066* (K). **P. ebracteolatus** Hiern vel aff.: CAMEROON. *Davis et al. 3008* (K). **P. fragrans** (Wall. ex Hook.f.) J.-F. Leroy: BURMA. *Griffith 5781* (K), *Helfer 3016* (K), *Kerr 21617* (K). **P. horsfieldianus** (Miq.) J.-F. Leroy: JAVA. *Horsefield 45* (K). LESSER SUNDA, BABAR I. *Riedel s.n.* (K). **P. lebrunianus** (R. Germ. & Kesler) J.-F. Leroy ex Bridson: CONGO-KINSHASA. *Callens 3176* (K), *Louis 5636* (K), *6326* (K). **P. leroyi** Bridson: ETHIOPIA. *Gereau et al. 1416* (K), *Gilbert 4154* (K). UGANDA. *Wilson 911* (K). **P. mabesae** (Elmer) J.-F. Leroy: PHILIPPINES. *Elmer 6405* (K), *McGregor 32422* (K), *Ramos 32840* (K). **P. malabaricus** Sivar., Biju & P. Mathew: INDIA. *Wight 1431* (K), *s.n.* (K). **P. melanocarpus** (Hiern) J.-F. Leroy: ANGOLA. *Gossweiler 4796* (K), *Welwitsch 3177* (K), *3180* (K). **P. merguensis** (Ridl.) J.-F. Leroy: THAILAND. *Kerr 14290* (K), *15338* (K), *Schmidt 619a* (K). **P. semsei** Bridson: TANZANIA. *Luke 4845* (K), *Rodgers s.n.* (K), *Semsei 3400* (K). **P. travancorensis** (Wight & Arn.) J.-F. Leroy: SRI LANKA. *Thwaites 2458* (K), *Walker 1466* (K), *Worthington 2208* (K). **P. wightianus** (Wall. ex Wight & Arn.) J.-F. Leroy: SRI LANKA. *Cooray 68102006R* (K), *Kostermans 24902* (K), *Mueller-Dombois 50140* (K).

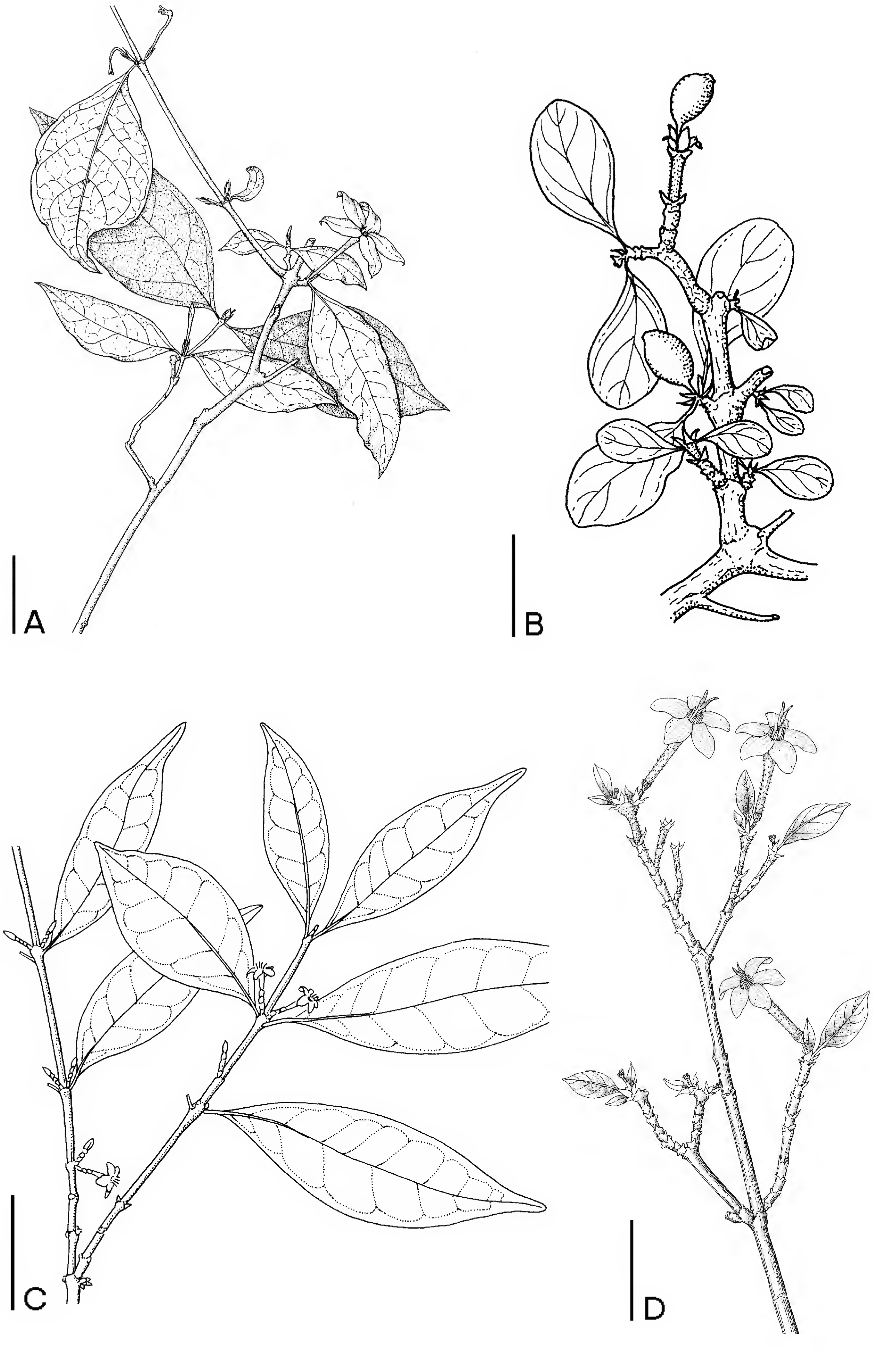


Figure 1. Shoot architecture in *Coffea* and *Psilanthus.* —A. *Psilanthus semsei* (*Psilanthus* subg. *Afrocoffea*), reproduced from Bridson (1982). —B. *Coffea rhamnifolia* (*Coffea* subg. *Baracoffea*), reproduced from Bridson (1982). —C. *Coffea minutiflora* (*Coffea* subg. *Coffea*). —D. *Coffea* sp. nov. 4 (*Coffea* subg. *Baracoffea*). A *Semsei 3400,* B *Hemming 396,* C *Capuron SF-23553,* D *Bisset M 13.* Scale bars: A, 3 cm; B–D, 2 cm. Drawn by D. Bridson (A & B) and L. T. Smith (C & D).

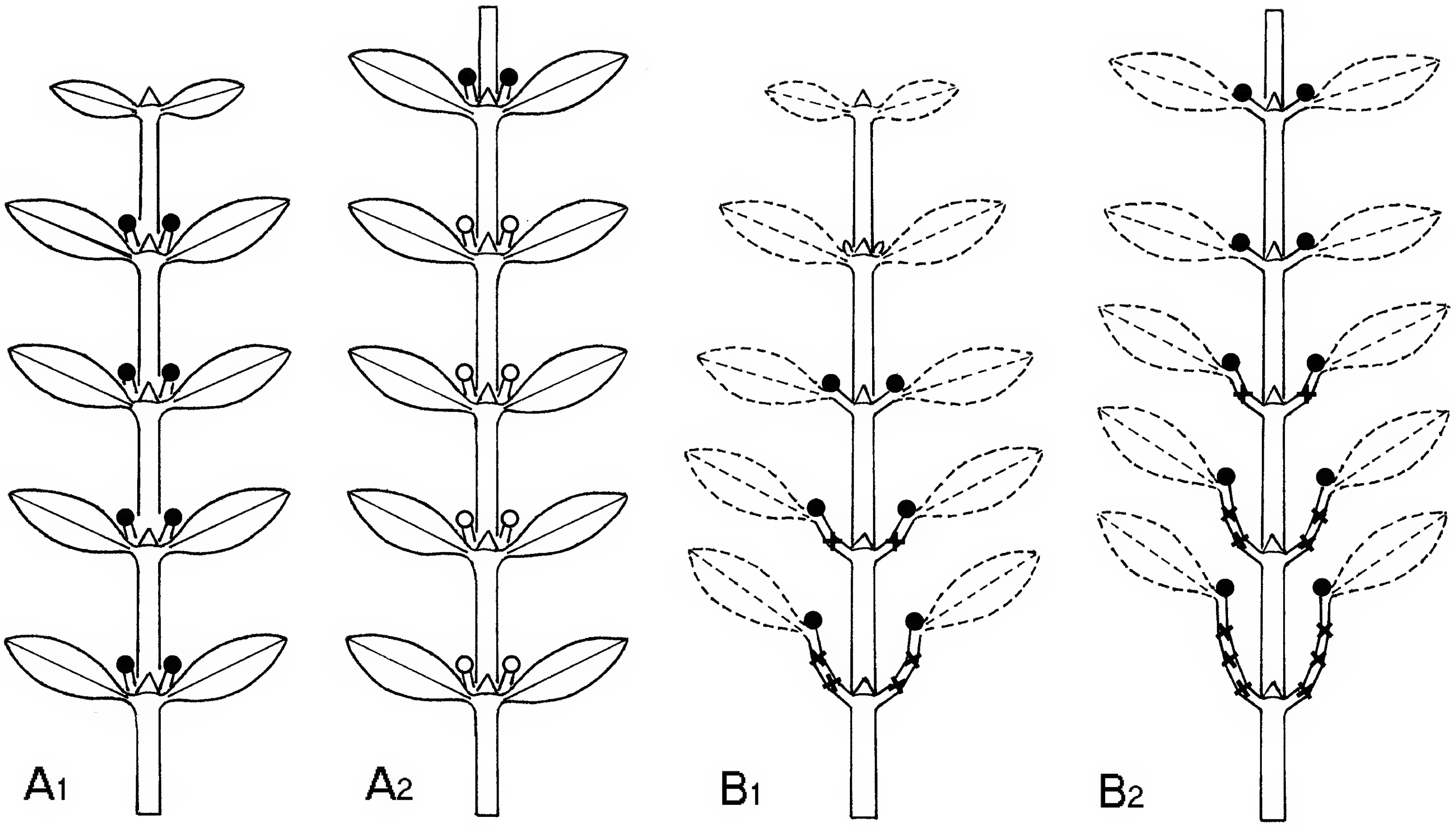


Figure 2. Shoot architecture models. A. Determinate inflorescences (e.g., *Coffea* subg. *Coffea*) shoot architecture not influenced by flowering. B. Indeterminate inflorescences (e.g., *Coffea* subg. *Baracoffea*). —A1. Flowering branch in first year; black circles represent flower(s), triangles represent stipules and shoot apex. —A2. The same shoot in the following year; open circles represent previous season's determinate inflorescences. —B1. Flowering branch in first year; black circles represent flower(s), triangles represent stipules and shoot apex, black crosses represent seasonal activity of lateral meristems, dotted outlines represent leaves (usually produced after flowering). —B2. The same shoot in the following year. See Appendix 1, Character 2 (Shoot architecture), for further information. Drawn by S. Dawson.

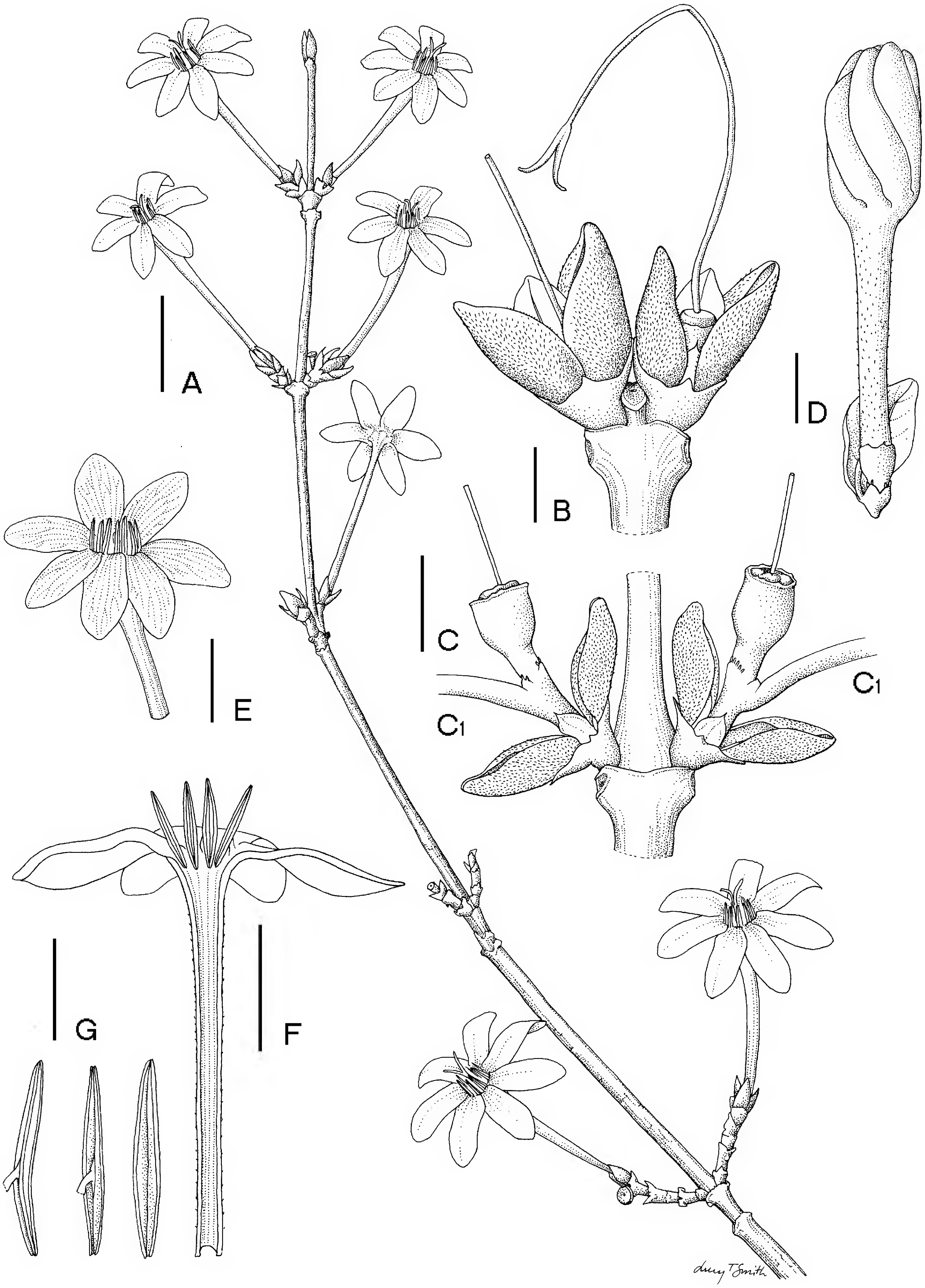


Figure 3. *Coffea* sp. nov. 1 (*Coffea* subg. *Baracoffea*). —A. Flowering shoot. —B. Inflorescence (immature, with corollas removed). —C. Inflorescence (mature, corollas fallen); C1. Petiole-like base of foliar lobe. —D. Flower bud, with upper calyculus. —E. Corolla, upper part of tube. —F. Corolla (longitudinal section). —G. Stamens. A–F, *Rakotonasolo RNF 240.* Scale bars: A, 2 cm; B, 3 mm; C, D, G, 5 mm; E, F, 1 cm. Drawn by L. T. Smith.

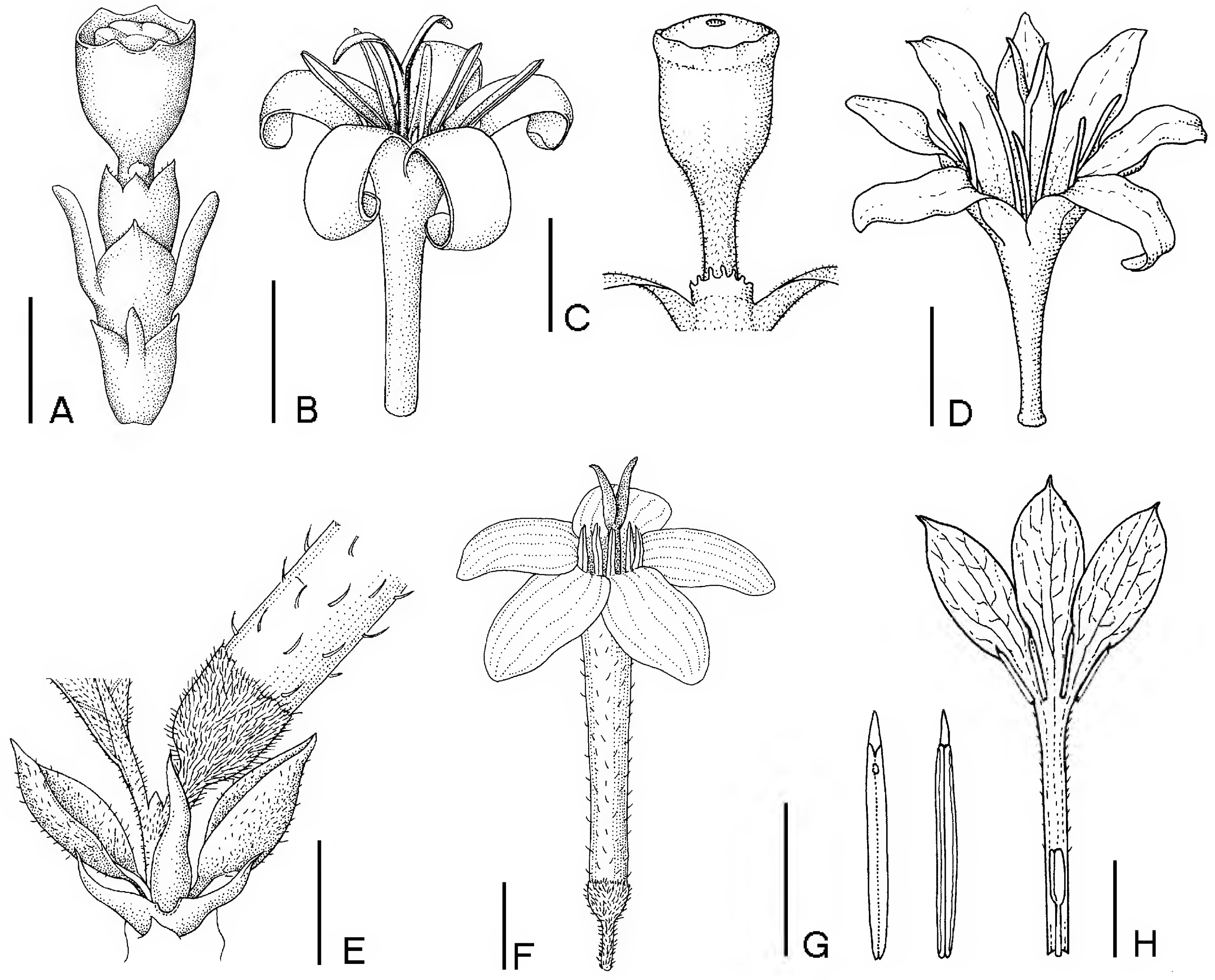


Figure 4. Inflorescence units and flowers of *Coffea* and *Psilanthus.* —A. *Coffea ratsimamangae* (*Coffea* subg. *Coffea*), calyculi and calyx; inflorescence unit formed from three calyculi. —B. *Coffea ratsimamangae,* flower. —C. *Coffea rhamnifolia* (*Coffea* subg. *Baracoffea*), upper (3rd) calyculus and calyx; upper calyculus showing petiole-like bases of foliar lobes. —D. *Coffea rhamnifolia,* flower. —E. *Coffea* sp. nov. 4 (*Coffea* subg. *Baracoffea*), calyculi, calyx, and base of corolla; inflorescence unit consisting of three calyculi (stipular lobes of basal (1st) calyculus fallen. —F. *Coffea* sp. nov. 4, flower. —G. *Psilanthus semsei* (*Psilanthus* subg. *Afrocoffea*), anthers; showing point of filament attachment and sterile apical appendage. —H. *Psilanthus semsei,* corolla dissection; showing length of style and position of style lobes. Scale bars: A, C, 2 mm; E, 3 mm; B, F, G, 5 mm; D, H, 1 cm. Drawn by D. Bridson (C, D, G & H) and L. T. Smith (A, B, E & F).

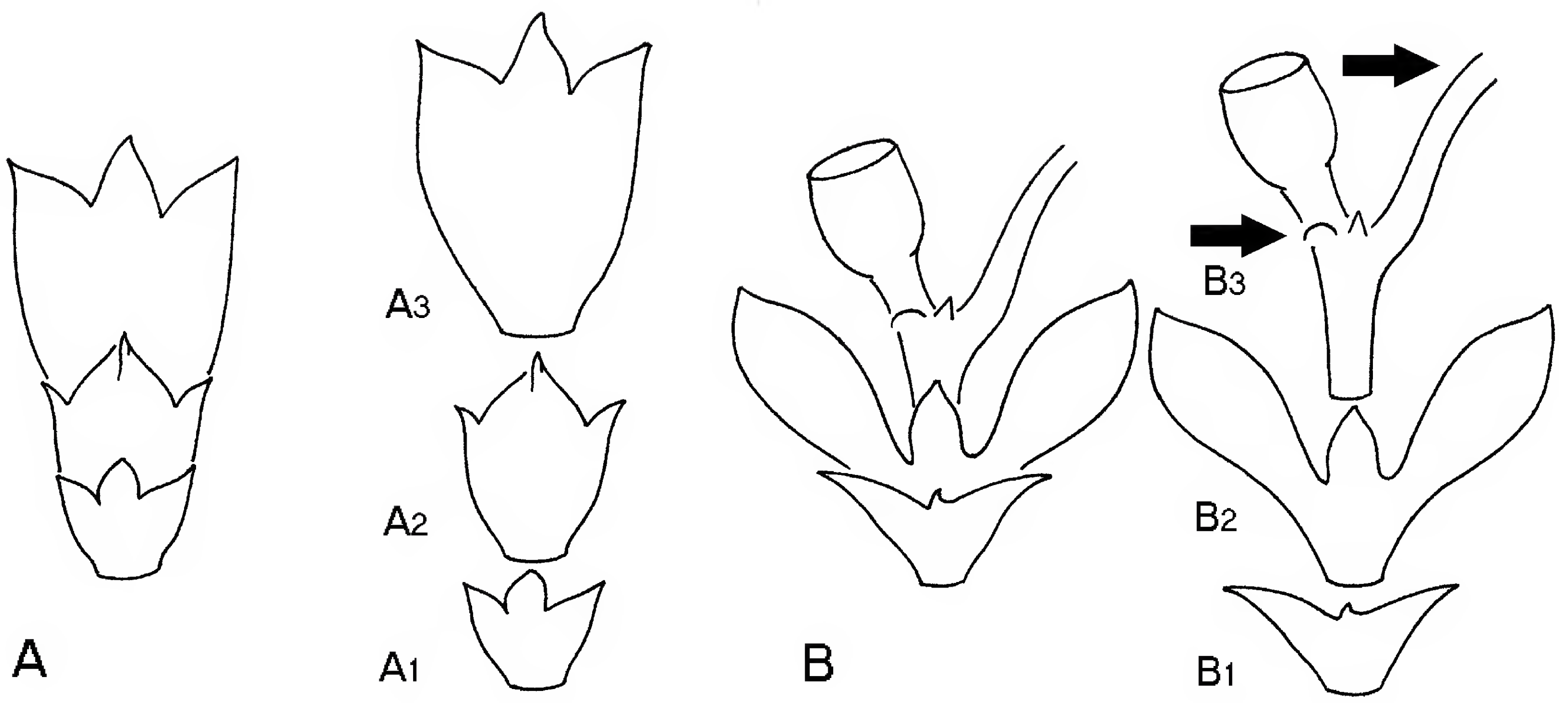


Figure 5. Diagrammatical representation of inflorescence units in *Coffea* subg. *Coffea* and *Coffea* subg. *Baracoffea.* —A. Inflorescence unit type of *Coffea* subg. *Coffea;* A1 basal (1st) calyculus, A2 middle (2nd) calyculus, A3 upper (3rd) calyculus. —B. Inflorescence unit type of *Coffea* subg. *Baracoffea;* B1 basal (1st) calyculus, B2 middle (2nd) calyculus, B3 upper (3rd) calyculus and calyx; arrows indicate vestiges of second foliar lobe (left) and petiole-like base of foliar lobe (right). Drawn by S. Dawson.

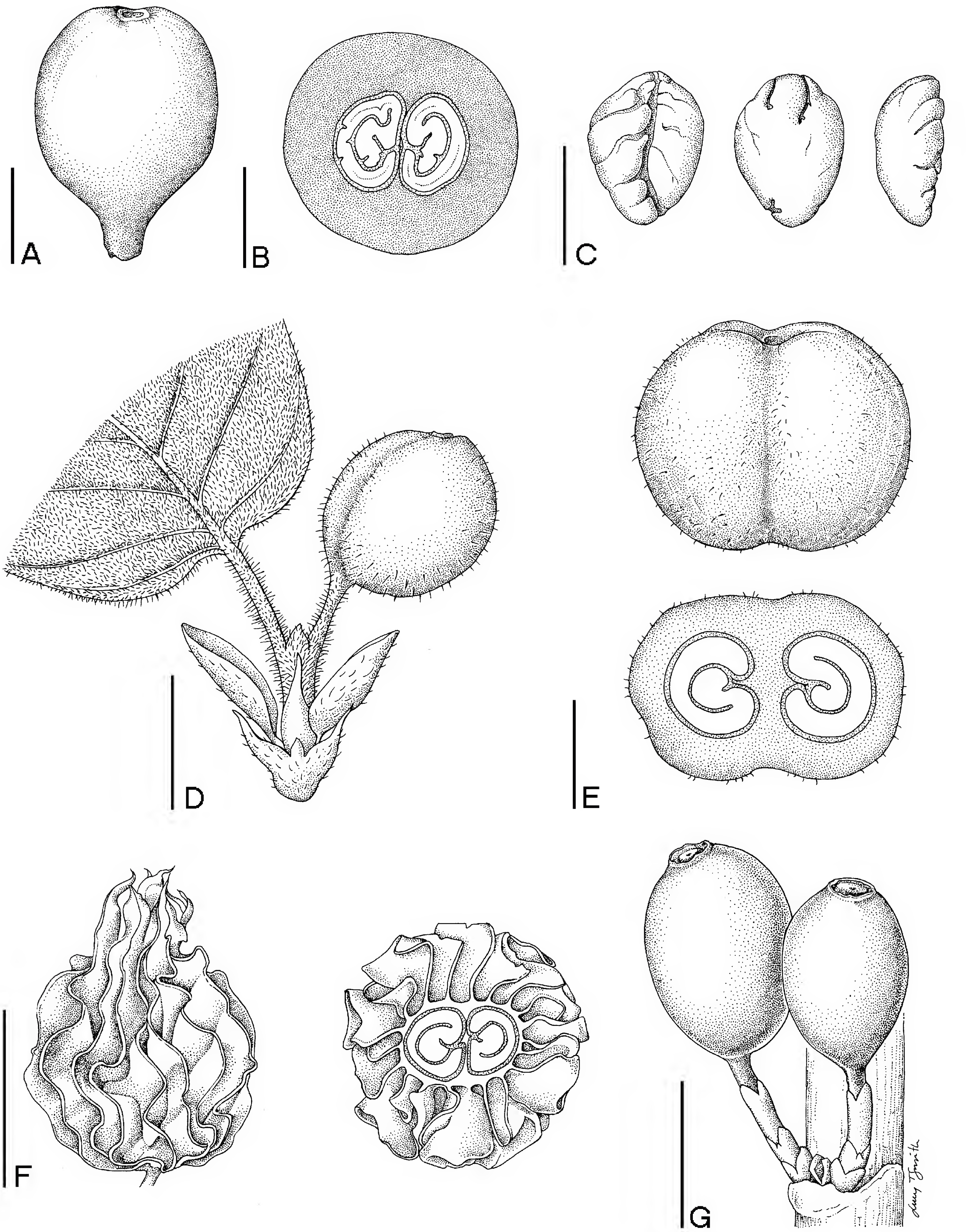
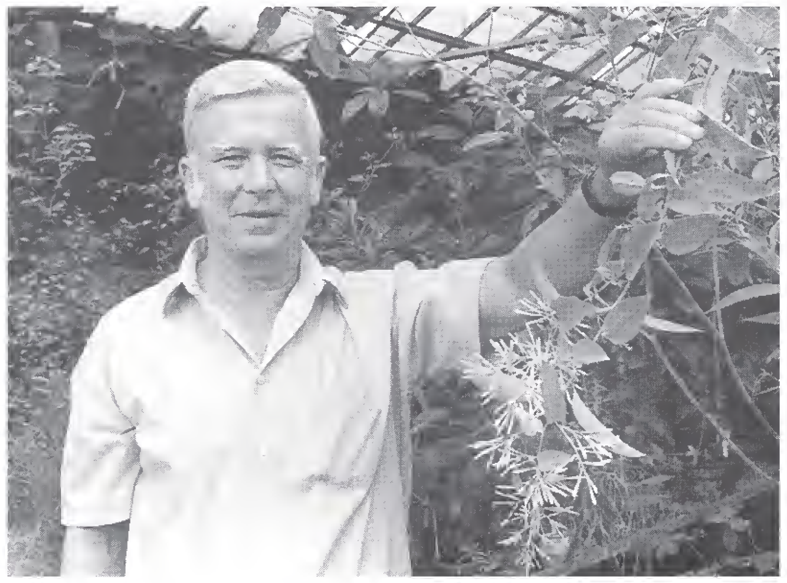


Figure 6. Fruit and seed morphology of *Coffea* subg. *Coffea* and *Coffea* subg. *Baracoffea*. —A. *Coffea* sp. nov. 2 *(Coffea* subg. *Baracoffea),* fruit. —B. *Coffea* sp. nov. 2, fruit in transverse section. —C. *Coffea* sp. nov. 2, seed in adaxial, abaxial, and side views (left to right). —D. *Coffea* decaryana (*Coffea* subg. *Baracoffea*) infructescence; three calyculi and young fruit (fruit opposes leaf-like foliar lobe). —E. *Coffea decaryana,* fruit with transverse section (below). —F. *Coffea* sp. nov. 3 (*Coffea* subg. *Baracoffea*), fruit with transverse section (right). —G. *Coffea homollei* (*Coffea* subg. *Coffea*), infructescence; each fruit with three calyculi. Scale bars: A, F, 2 cm; B, C, 1 cm; G, 5 mm; D, E, G, 5 mm. Drawn by L. T. Smith.

evolution of the family. He organized scientific meetings, carried out 25 field expeditions, and published about 144 scientific contributions.

This volume features a collection of scientific contributions by D'Arcy's friends and colleagues that form a fitting memorial to the life of this influential taxonomist. In addition to Solanaceae, there are contributions on genera of Araceae, Myrtaceae, Rubiaceae, and Rutaceae, from the perspectives of taxonomy, floristics, cytology, and other fields that reflect D'Arcy's broad interests. Thirteen new species are described. In addition, a biography and publication list summarize his life. A list of taxa described by him, and described in his honor, are also included.



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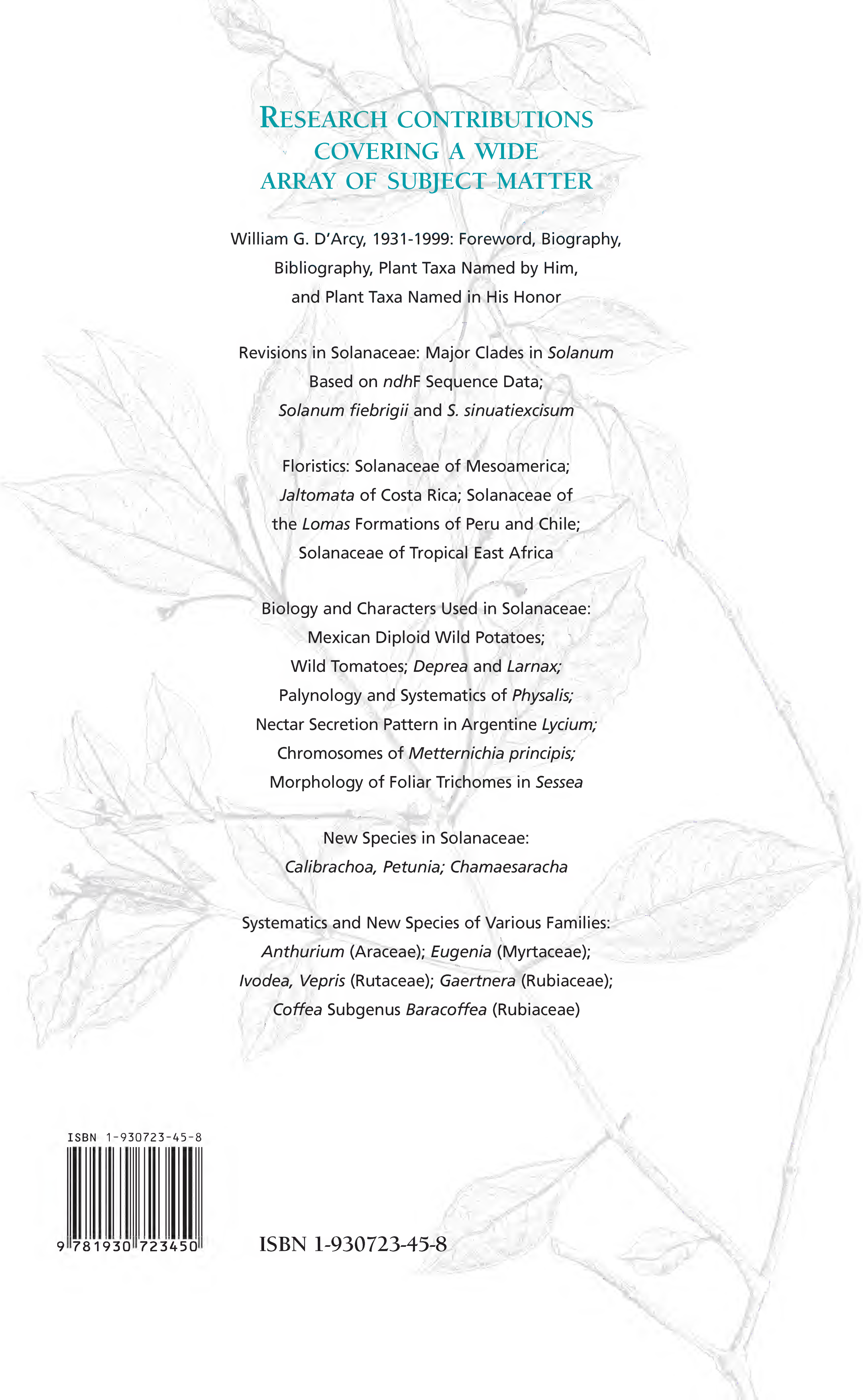

RESEARCH CONTRIBUTIONS COVERING A WIDE ARRAY OF SUBJECT MATTER

William G. D'Arcy, 1931-1999: Foreword, Biography, Bibliography, Plant Taxa Named by Him, and Plant Taxa Named in His Honor

Revisions in Solanaceae: Major Clades in *Solanum* Based on *ndh*F Sequence Data; *Solanum fiebrigii* and *S. sinuatiexcisum*

Floristics: Solanaceae of Mesoamerica; *Jaltomata* of Costa Rica; Solanaceae of the *Lomas* Formations of Peru and Chile; Solanaceae of Tropical East Africa

Biology and Characters Used in Solanaceae: Mexican Diploid Wild Potatoes; Wild Tomatoes; *Deprea* and *Larnax;* Palynology and Systematics of *Physalis;* Nectar Secretion Pattern in Argentine *Lycium;* Chromosomes of *Metternichia principis;* Morphology of Foliar Trichomes in *Sessea*

New Species in Solanaceae: *Calibrachoa, Petunia; Chamaesaracha*

Systematics and New Species of Various Families: *Anthurium* (Araceae); *Eugenia* (Myrtaceae); *Ivodea, Vepris* (Rutaceae); *Gaertnera* (Rubiaceae); *Coffea* Subgenus *Baracoffea* (Rubiaceae)

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